New Phyllolepids from Victoria and the Relationships of the Group

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(Communicated by A. RITCHIE)

Two new phyllolepids (Placodermi: Phyllolepidae), *Austrophyllolepis ritchiei,* gen. et sp. nov., and *Austrophyllolepis youngi*, gen. et sp. nov., are described from the Frasnian lacustrine shales near Mt Howitt, Victoria. *Austrophyllolepis* gen. nov. is distinguished from *Phyllolepis* by the presence of a posterior median ventral plate, and by the shape of the marginal plate. *Austrophyllolepis ritchiei,* gen. et sp. nov. is a broad species with a mature armour equally as long as broad whereas *A. youngi* is characterized by having a slender armour, noticeably different from *A. ritchiei* in the proportions of the preorbital, paranuchal, nuchal, median dorsal, anterior lateral, anterior ventrolateral and posterior ventrolateral plates. Both species are represented by individuals in all stages of growth. New anatomical features described for phyllolepids include the visceral surface of the headshield and dorsal endocranial form, gnathalia, parasphenoid, cheek plate, otoliths, axial skeleton, tail and pelvic girdle. It is suggested that the phyllolepids are specialized actinolepidoid euarthrodires because of characters shared in the endocranium, skull roof and trunkshield. The order Phyllolepida (Stensiö, 1934) is made redundant, the family Phyllolepidae (Woodward, 1891) is placed in the infraorder Phyllolepidi of the suborder Actinolepidoidei (Miles and Young, 1977).

INTRODUCTION

Phyllolepids were dorsoventrally flattened placoderm fishes which have been recorded from continental deposits of Late Devonian age from east Greenland (Heintz, 1930; Stensiö 1934, 1936, 1939), Scotland (Agassiz, 1844; Woodward, 1914, 1920), Belgium (Leriche, 1931), Baltic Russia (Vasilauskas, 1963), North America (Newberry, 1899), Antarctica (Ritchie, 1972), Australia (Hills, 1929, 1932, 1935, 1958b) and Turkey (Dr P. Janvier, pers. comm. 1982). The restricted time range of phyllolepids in the northern hemisphere has made them biostratigraphically useful as zone fossils for part of the Famennian. In Australia phyllolepids are known from Frasnian and Famennian strata (Young, 1974; Fergusson *et al.,* 1979; Long, 1983). Despite the widespread distribution of phyllolepids their structure is known only from a few articulated specimens of *Phyllolepis (P. orvini, P. woodwardi)* and the relationships of the group within the Placodermi have up until now been based only on the features of the dermal armour. Prior to the detailed work of Stensiö phyllolepids were considered by some workers to be agnathans similar to the heterostracan *Drepanaspis* (Woodward, 1914, 1920; Heintz, 1930). The material described in this paper from Mt Howitt, Victoria, reopens the question of phyllolepid relationships within the placoderms in the light of new anatomical observations. Current placement of the phyllolepid placoderms is as a sister group to the antiarchs and euarthrodires (Miles and Young, 1977; Young, 1980; Denison, 1978). Denison (1975, 1978) expresses the opinion that phyllolepids were derived from primitive euarthrodiran stock.

The Mt Howitt fossil site has yielded a diverse fauna of Frasnian freshwater fishes including the placoderms *Bothriolepis gippslandiensis, B. cullodenensis, B. fergusoni, Groenlandaspis* sp. (Long, 1982, 1983a), *Austrophyllolepis ritchiei,* gen. et sp. nov, and *A.*

youngi, gen. et sp. nov; a diplacanthoid acanthodian, *Culmacanthus stewarti* (Long, 1983b), acanthodiform acanthodians similar to *Acanthodes* (Long, 1983c), new genera of dipnoans with bodies resembling *Fleurantia* and *Scaumenacia* (Marsden, 1976), a new genus of palaeoniscoid, and new genera of crossopterygians belonging to both the Osteolepiformes and Porolepiformes. There are no invertebrates from the site although plant remains are common, mostly being lycopsids. The geological setting and taphonomy of the site is discussed by Marsden (1976) and Long (1982b). The age of the locality and correlations with other Late Devonian ichthyofaunas of southeastern Australia was treated by Long (1983a).

The Mt Howitt specimens were prepared both manually and with dilute hydrochloric acid to remove the friable bone so that latex casts could be made. As the respective plates of *Phyllolepis orvini* have been described in detail by Stensiö (1934, 1936) I have omitted lengthy descriptions of each plate of the new material where it is essentially similar to that of *Phyllolepis*. The following descriptions summarize the proportional differences between the species leaving the illustrations to show form and variation of individual plates. This approach has been successfully utilized recently in the series of papers on the Gogo placoderms by Miles and Dennis (1979) and Dennis and Miles (1979, 1980, 1983). The reliability of comparisons with other phyllolepids is shown by the graph (Fig. 24) recording taxa versus material known.

Specimens are housed in the Museum of Victoria, Melbourne. Throughout the text breadth and length are abbreviated as B and L respectively, and plate names are abbreviated in accordance with the text figures.

In Australia phyllolepid plates have been recorded from Taggerty (Hills, 1929) and the South Blue Range in Victoria (Hills, 1936); from Harvey's Range north of Parkes (Hills, 1932) and near Eden in New South Wales (Fergusson *et al.*, 1979); and from the Dulcie Range in the Northern Territory (Hills, 1958). Unpublished finds of phyllolepids from Australia include isolated plates from Freestone Creek, Tatong and Snowy Bluff in Victoria, and from the Jemalong Range, and Khan Yunis in New South Wales. Aside from *Placolepis budawangensis* (Ritchie, 1984) and the Mt Howitt phyllolepids, all other material from Australia is of isolated plates.

HOMOLOGY OF PHYLLOLEPID PLATES

The three anteriormost pairs of headshield plates in phyllolepids have been interpreted in two ways. Before describing the new material systematically it is necessary to clarify the homology of these bones. Criteria for homology used here are outlined by Wiley (1981: 130).

Stensiö (1969) regards the anteromesial pair of headshield plates as true preorbital plates (PRO) whereas Denison (1975, 1978) considers these as possibly being postnasal plates (PN). Both PRO and PN plates carry a section of the supraorbital sensory line groove. I regard this pair of plates as being PRO plates homologous to those of euarthrodires, petalichthyids and some palaeacanthaspidoids because of their situation anterior to the nuchal (or centronuchal; Nu) plate, and their mesial contact. In most euarthrodires, *Wuttagoonaspis*, some petalichthyids and *Kimaspis* the PRO plates are in mesial contact with the central plates (Ce) or centronuchal area posteriorly (Fig. 1). Orbital position is not reliable for identification of the PRO plates as it is a variable feature of most placoderm groups. In euarthrodires the orbit is commonly situated between the PRO and postorbital (PTO) plates, yet in *Actinolepis* (Fig. 1) it is contained by the PTO and PN plates (Mark-Kurik, 1973), and in *Homostius* it is bounded by Ce plates separating the PRO and PTO plates (Obruchev, 1964). In the rhenanid *Brindabellaspis* there is a marginal plate (MG) separating the PRO and PTO plates (Young, 1980). The position of the orbit of phyllolepids is below the anterior half of the PTO
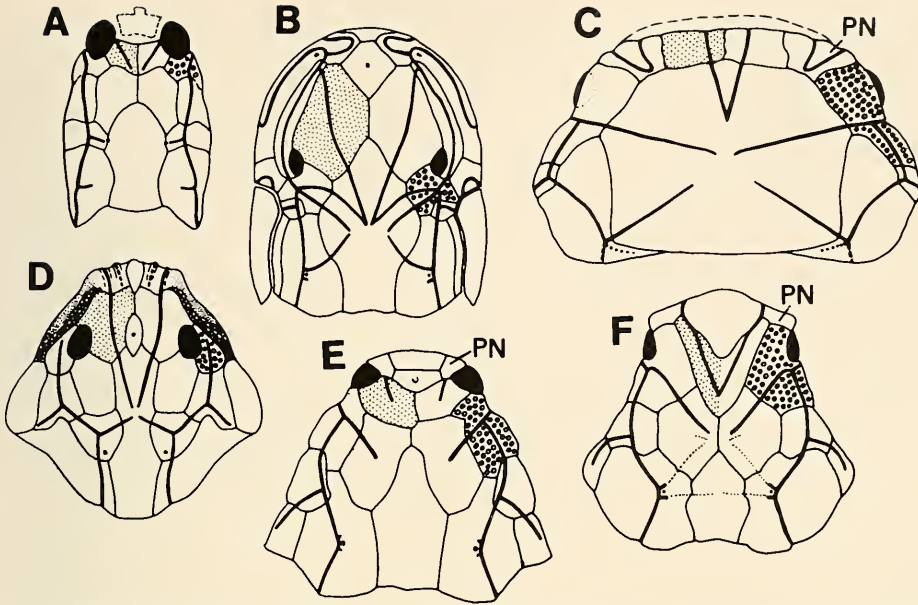
Fig. 1. Homology of the preorbital, postnasal and postorbital plates. Left preorbital plate stippled, right postorbital plate shaded with circles, orbital area in black and postnasal plate labelled PN. **A.** *Kimaspis* (after Mark-Kurik, 1973b). **B.** *Wuttagoonaspis* (after Ritchie, 1973). **C.** *Austrophyllolepis ritchiei* gen. et sp. nov. **D.** *Lunaspis* (after Gross, 1961). **E.** *Kujdanowiaspis* (after Stensiö, 1945). **F.** *Actinolepis* (after Mark-Kurik, 1973a). Note the position of the postnasal plate in *Kujdanowiaspis* and *Actinolepis* and the proposed homology of this plate in *Austrophyllolepis.* The predicted position of the cartilaginous rhinocapsular in *Austrophyllolepis* is represented by a broken line. Not to scale.

plate as indicated by the supraorbital vault described below. As such it is not divided between two plates due to its small size, as also occurs in *Actinolepis.* I conclude that true PRO plates in placoderms are recognized by the presence of a section of the supraorbital sensory line groove, and are situated anterior or anterolateral to the centronuchal area, often in mesial contact with each other or separated by extensions of the pineal, rostropineal or centronuchal plate areas. They most frequently border the anterior or dorsal rim of the orbit, but not always, as in *Actinolepis* and phyllolepids.

The second pair of plates flanking the nuchal plate of phyllolepids have been interpreted as dermosphenotics (or equivalent to the anterior division of the PTO plate of euarthrodires) by Stensiö (1969: 357) and as ?PRO plates by Denison (1978: 41). To evaluate the homology of these plates it is necessary to confirm that the plates contacting them posteriorly are true PTO plates, thus eliminating the first hypothesis. The third pair of marginal plates are regarded as PTO plates because they bear the triple point junction of the central sensory line canal, infraorbital sensory line canal and main lateral line canal, and they possess a supraorbital vault for the optic capsule and have ventral grooves for both the anterior and posterior postorbital endocranial processes. In primitive euarthrodires the PTO plates bear the triple point junction of the sensory line canals, part of the supraorbital vault (or most of it in *Actinolepis*), and have a groove for the anterior postorbital process of the endocranium (*Dicksonosteus,* Goujet, 1975; *Kujdanowiaspis,* Stensiö, 1963). The PTO plate of most placoderms bears the triple point junction of the sensory line canals and part of the orbital border, although relationships to the underlying endocranial processes are variable (see Young, 1980).

Accepting that the third pair of phyllolepid headshield plates are PTO plates (also corroborated by Denison, 1978, and partly by Stensiö, 1969) the second pair of plates situated between the PRO and PTO plates can be interpreted as PN plates by virtue of their position (Fig. 1). PN plates in placoderms are situated lateral to the nasal capsules or their dermal bone cover (rostral plates or rostropineal plates). In several actinolepidoid and phlyctaenioid euarthrodires the rhinocapsular ossification which continued the nasal capsules was independently ossified from the rest of the endocranium, and is often found separated from the post-ethmoid ossification (Jarvik, 1980, vol. 1: 374). Examples of this are *Baringaspis* (Miles, 1973), *Kujdanowiaspis* (Stensiö, 1945), *Simblaspis* (Denison, 1958), *Aggeraspis* (Gross, 1962) and *Gaspeaspis* (Pageau, 1969). From the excellent preservation of the Mt Howitt phyllolepids it is evident that there was not an ossified rhinocapsular bone; instead it was probably cartilaginous like the postethmoid region of the endocranium. The rhinocapsular of phyllolepids would have articulated below the paired preorbital plates, as it does for all euarthrodires with an independent rhinocapsular bone. The PN plates are located on the anterolateral borders of the headshield in phyllolepids and *Actinolepis* (Mark-Kurik, 1973) clearly where the lateral limitations of the rhinocapsular would be expected. The unusual inflexion of a sensory line canal on this plate in phyllolepids is not difficult to explain if the PN plate changes its position from that of primitive euarthrodires, anterior to the PRO plate, to being lateral or anterolateral to the PROs causing a doubling up of the supraorbital canal. Alternatively the looped sensory canal of the PN plate may be a specialization of phyllolepids for increasing the dorsal sensory line length. A similar loop of the sensory line canal in this position is well known in *Chimaera* (Stensiö, 1947: fig. 10).

The remaining plates of the phyllolepid dermal armour are directly homologous with those of other placoderms, and especially similar to those of primitive euarthrodires (Stensiö, 1934, 1936, 1969).

SYSTEMATIC DESCRIPTIONS
Family PHYLLOLEPIDAE Woodward 1891
AUSTROPHYLLOLEPIS gen. nov.

Phyllolepis   Marsden, 1976: 122 (from Mt Howitt).
Phyllolepis   Long, 1982a: 63 (from Mt Howitt), figs 5D, 6C.
Phyllolepis   Long, 1982b: fig. 1 (from Mt Howitt only).
Phyllolepis   Long, 1983a: 297, figs 2, 3 (from Mt Howitt only).
Phyllolepid   Long, 1983c: 22, fig 7.

Etymology: From the Latin 'australis' southern, combining form for the generic name *Phyllolepis,* pertaining to the Australian location of this phyllolepid.

Diagnosis: Medium-sized phyllolepid placoderms possessing a posterior median ventral plate which is overlapped by the anterior and posterior ventrolateral plates. A small suborbital plate firmly articulates with an ossified process below the postorbital plate. Anterior median ventral plate absent. Marginal plate broad with an external B/L index close to 36. The main lateral line sensory canal enters the paranuchal plate from the marginal plate at a point between 68-72% of the total length of the paranuchal plate. The shape and overlap relationships of the remaining plates are as for *Phyllolepis*.

Type species: Austrophyllolepis ritchiei sp. nov.

Remarks: The new genus is readily distinguished from the two other known phyllolepid genera, *Phyllolepis* and *Placolepis* (Ritchie, 1984), by the presence of a relatively large posterior median ventral plate (PMV). The paranuchal plate (PNu) of *Austrophyllolepis* differs from that of the other two genera by the position of entry of the lateral line canal
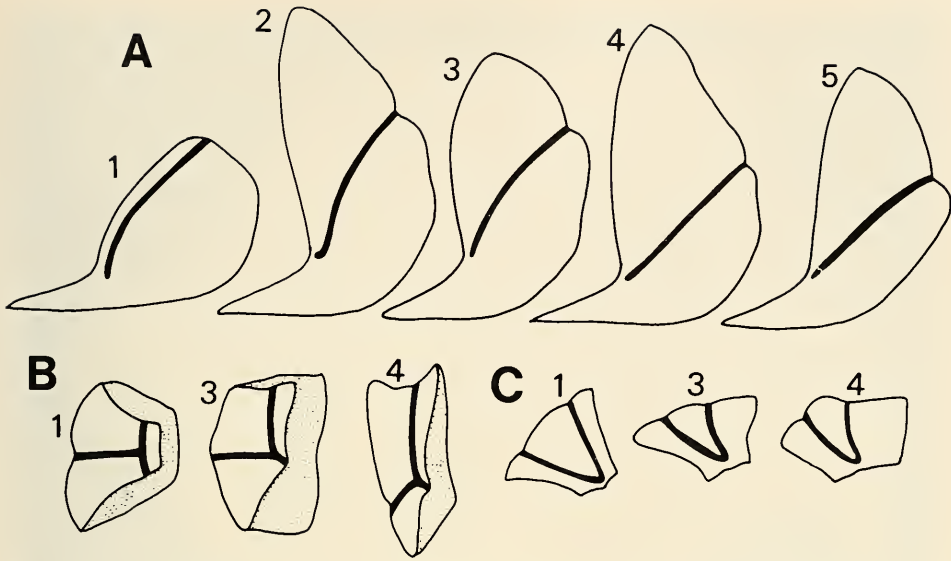
Fig. 2. Differences between the right paranuchal (A), left marginal (B) and left postnasal plates (C) in various phyllolepids. **1.** *Placolepis budawangensis.* **2.** *Austrophyllolepis youngi,* gen. et sp. nov. **3.** *Austrophyllolepis ritchiei* gen. et sp. nov. **4.** *Phyllolepis orvini.* **5.** *Phyllolepis woodwardi.*

which enters the PNu at its anterior extent on *Placolepis* and about midway on *Phyllolepis* (Fig. 2). The anterior median ventral plate (AMV) is known only on *Phyllolepis woodwardi* (Stensiö, 1934) being inferred to be present in *P. orvini* by Stensiö (1936, 1939) despite its absence in the east Greenland material (which I had the opportunity to examine). It is more likely that the AMV plate was variably present in the genus. All the known species of the genus *Phyllolepis* (except for *P. delicatula* Newberry) are represented by anterior ventrolateral plates (AVL) which do not show embayment for a PMV plate. Consequently the presence of a well developed PMV plate in *Austrophyllolepis* separates this genus from both *Phyllolepis* and *Placolepis*. The small 'PX' bones of Stensiö (1936: 15) in *Phyllolepis woodwardi* are too small to be a well formed PMV plate and the posteromesial margin of the AVL plates are not noticeably embayed, only slightly displaced. It is probable that these are fragments of the axial skeleton which have slipped out of a gap in the ventral wall of the trunkshield (compare with the description of the axial skeleton of *Austrophyllolepis* given below).

As the small suborbital plate (SO) of *Austrophyllolepis* has not been observed on other phyllolepids it is retained as a generic feature until further information on the cheek of other species is known. In all other respects the dermal skeleton of *Austrophyllolepis* closely resembles that of *Phyllolepis*.

Austrophyllolepis ritchiei sp. nov.
Figs 1**C**; 2A-3, B-3, C-3; 3-7, 14**A**, **B**; 17; 18**C**; 19**B**, **C**; 23; 25**A**.

Etymology: After Dr Alex Ritchie, Australian Museum, Sydney.
Material: Holotype NMP 160721, a complete individual preserved as a mould of both dorsal and ventral surfaces, lacking the tail. NMP 160722, NMP 160723 imperfect headshields. NMP 160726, complete juvenile armour; NMP 160729 imperfect juvenile armour. NMP 160731, imperfect juvenile in ventral view only. NMP 160736, imperfect median dorsal plate. NMP 160737, headshield with jaws and parasphenoid.
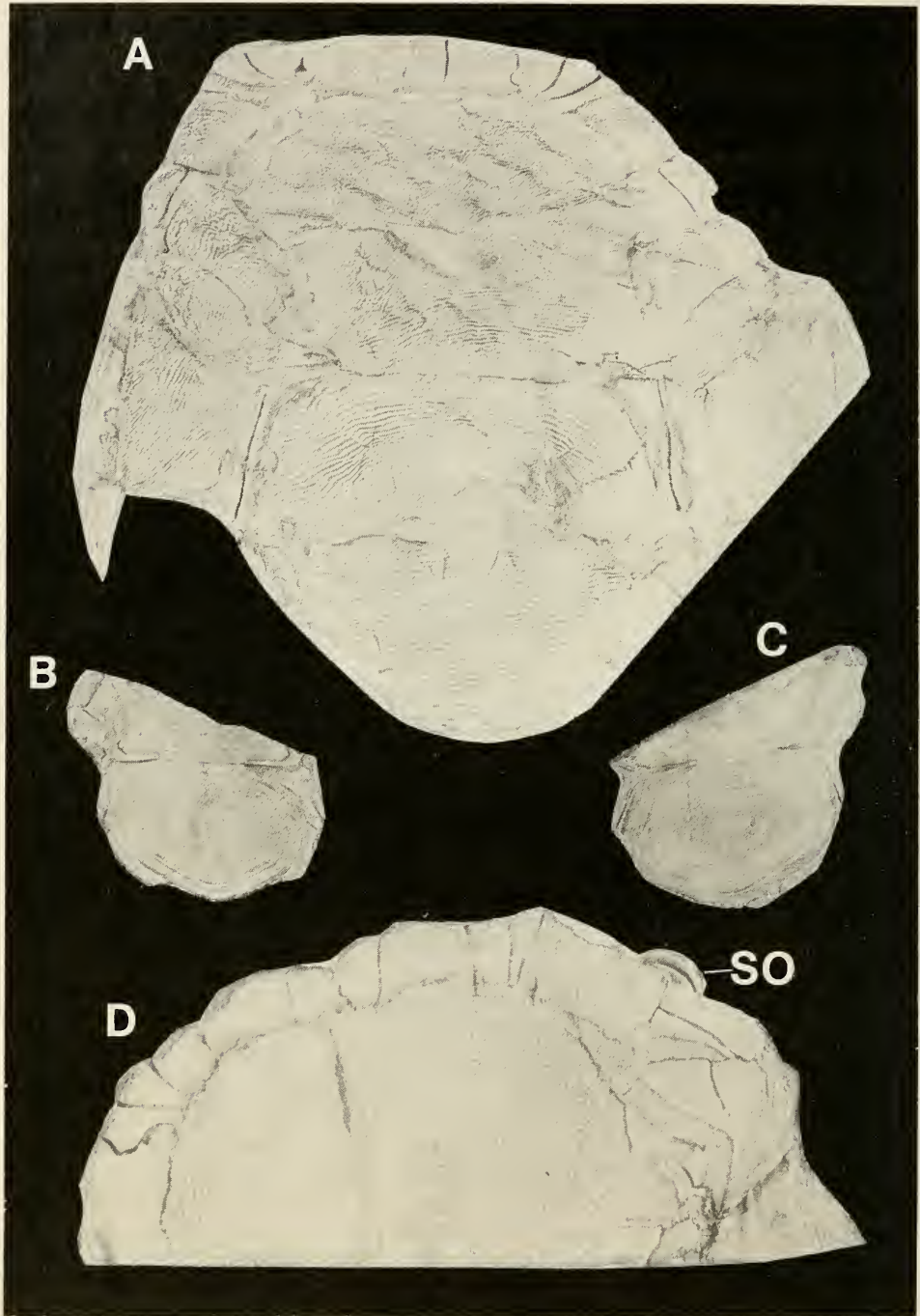
Fig. 3. Austrophyllolepis ritchiei gen. et sp. nov. **A**. Holotype, entire dermal armour in dorsal view, NMP 160721. **B, C**. Imperfect juvenile armour, dorsal view showing the internal mould **(B)** and external cast **(C)**, NMP 160729. **D**. Partial headshield in dorsal view, NMP 160722. All natural size. **A, D** are latex casts, **B** and **C** are actual specimens, all whitened with ammonium chloride. SO, suborbital plate.

NMP 160743, imperfect headshield. NMP 160748, imperfect headshield. NMP 160750, large complete individual with the tail. NMP 160753, disrupted large individual. NMP160756, imperfect headshield. NMP 160759, disrupted headshield. NMP 160763, imperfect ventral trunkshield.

Occurrence and age: From the main quarry in the lower mudstone of the Avon River Group section exposed along the upper Howqua River, Victoria (Marsden, 1976). Frasnian.

Diagnosis: An *Austrophyllolepis* having a maximum mid dorsal armour length around 200 mm. The mature dermal armour is as broad as long, being slighly broader in juveniles. Preorbital plate with an external B/L index close to 200; paranuchal plate has an external B/L index from 58-65; nuchal plates has a B/L index from 126-142; median dorsal plate has a B/L index from 122-145. Anterior ventrolateral plate with an anteromesial angle of 80-83 degrees, anterior division (the area perpendicular to the mesial margin at the anterior limit of the spinal margin) narrow, being close to 10% of the total plate length, overall B/L index around 90. Posterior ventrolateral plate has a B/L index close to 80.

Description: The form and proportions of the dermal armour can be seen in the figures, typified by the holotype (MV P160721; Figs 3**A**, 4**A**, 5). The headshield is characteristically broad with plate relationships similar to *Phyllolepis woodwardi.*

The preorbital plates (PRO) meet medially in an irregular suture. The median division of the PRO plate comprises one third of the total plate surface area. On the ventral surface the thickening below the supraorbital sensory line broadens anteriorly.

The postnasal plates (PN) have lightly convex anterior margins which are over twice the extent of the external posterior margins. As in the PRO plate there is a large thickening on the ventral surface below the V-shaped infraorbital canal groove. The anterior margin has a broad thick region of spongiose bone here, perhaps for attachment of the cartilaginous rhinocapsular. In both the PRO and PN plates there are many small pores close to the anterior margin.

The postorbital plate (PTO) is of the same shape as in *Phyllolepis;* unlike its equivalent in *Placolepis* it contacts the paranuchal plate (PNu). The junction of the infraorbital sensory line canal and the main lateral line canal is closer to the lateral margin of the plate rather than the medial margin as in *Phyllolepis.* Sometimes there is a short profundus sensory line canal present, as in NMP 160723 (Fig. 19**B**, pfc). On the ventral surface of the PTO plate there is a semicircular thickening of bone in the anterior half which I interpret as a supraorbital vault for the optic capsule (Fig 14**A**, sov; see discussion under new anatomical observations). The posterior half of the ventral surface shows a well defined ridge running parallel to the lateral margin of the plate for the posterior postorbital process of the endocranium (pr.ppo). Between this ridge and the supraorbital vault is a central thickening of bone apparently bearing a groove or foramen (it is difficult to determine from latex casts, but is thought to be a foramen in *Placolepis,* Ritchie, 1984). The position of this ridge between the orbit and the posterior postorbital process suggests that it is an ossified extension of the anterior postorbital process of the endocranium. If this is correct then the foramen would have housed the ramus hyomandibularis branch of the seventh cranial nerve, which runs to the epihyal element behind this process in euarthrodires (Goujet, 1975).

The marginal plate (MG) differs from that of *Phyllolepis* only in being slightly broader and proportionately a bit larger (Figs 2, 25). The groove for the posterior postorbital process of the endocranium continues posteriorly onto the MG plate where it terminates, as indicated by a transverse ridge meeting the groove to form a corner which enclosed the tip of the endocranial process.

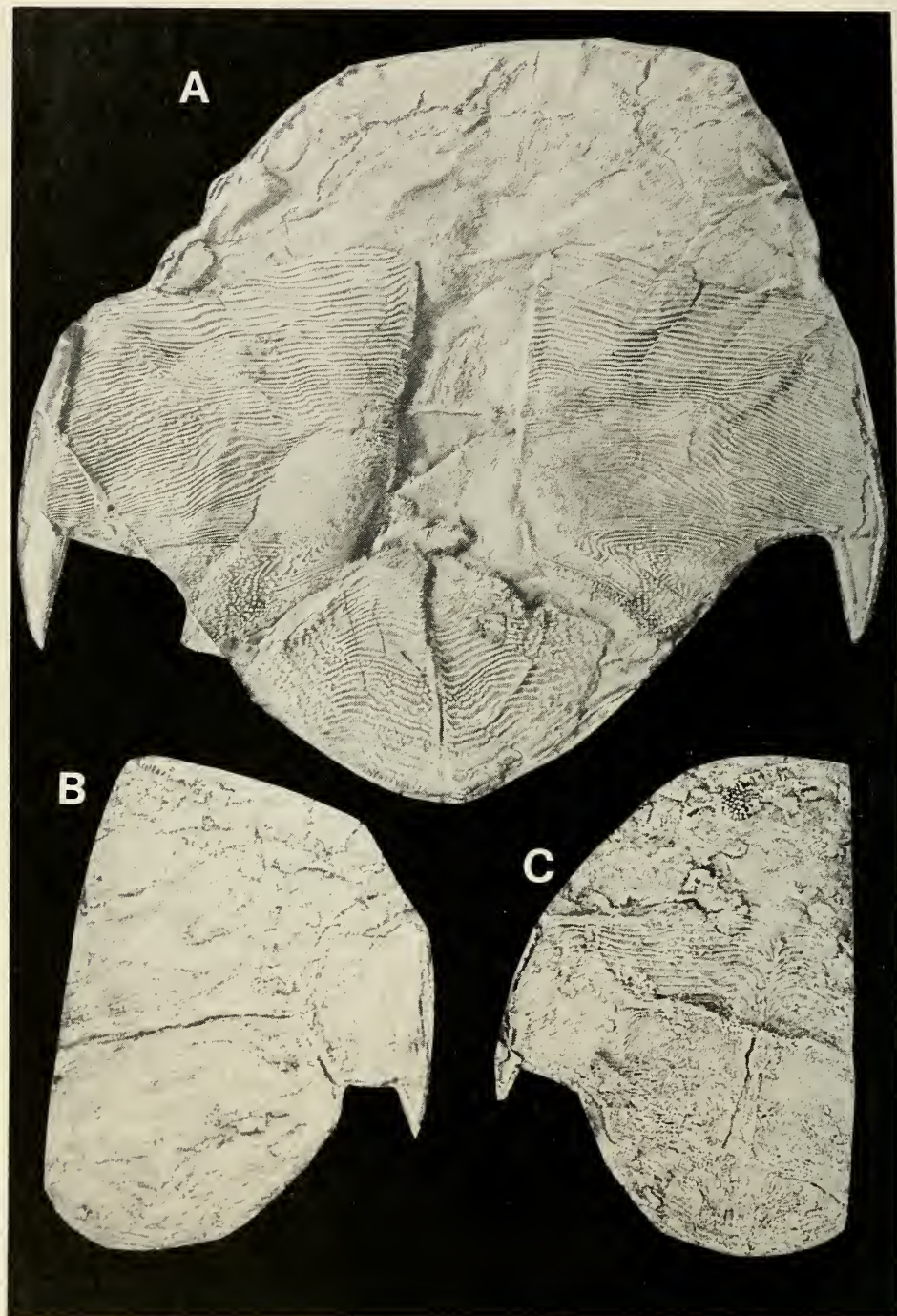The paranuchal plate (PNu) differs from that of *Phyllolepis* only in the position of

Fig. 4. Austrophyllolepis ritchiei gen. et sp. nov. **A.** Holotype, entire armour in ventral view, NMP 160721, natural size. **B, C.** Juvenile armour in dorsal **(B)** and ventral views **(C)**, NMP 160726, ×3. Latex casts whitened with ammonium chloride.
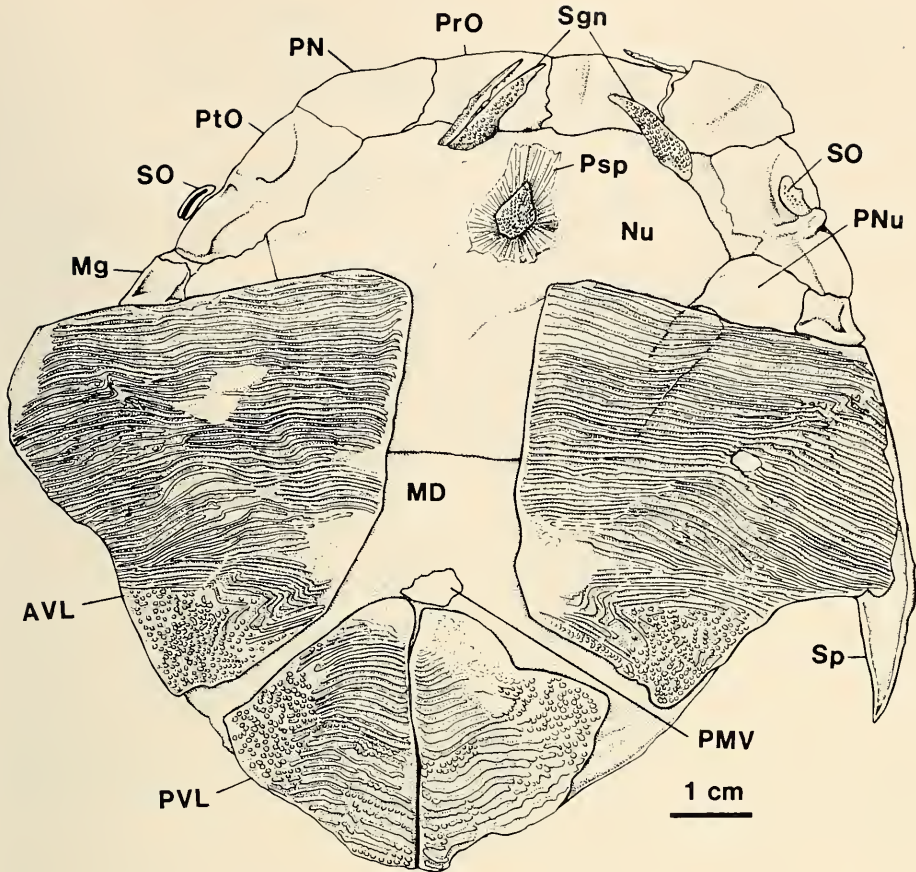
Fig. 5. Austrophyllolepis ritchiei gen. et sp. nov. Holotype in ventral view showing internal surface of head-shield, jaws and parasphenoid. AVL, anterior ventrolateral plate; MD, median dorsal plate; Mg, marginal plate; Nu, nuchal plate; PMV, incomplete posterior median ventral plate; PN, postnasal plate; PNu, paranuchal plate; Pro, preorbital plate; Psp, parasphenoid; PtO, postorbital plate; PVL, posterior ventrolateral plate; Sgn, supragnathals; SO suborbital plate; Sp, spinal plate.

entry of the main lateral line canal as diagnosed above. The ventral surface of the PNu has a prominent crista for the craniospinal process of the endocranium, as in *Phyllolepis orvini* (Stensiö, 1934: pl. 5, fig. 3; noted by Young, 1980).

The nuchal plate (Nu) has similar shape and overlap relations to that of *Phyllolepis*. The anterior margin has a slight median convexity between the supraorbital sensory line canals which meet at a point 72-76% of the total plate length from the posterior margin. External contact margins for the PN, PTO and PNu plates are clearly delineated. Only the supraorbital and central sensory line canals are clearly defined, although the posterior pit line canal may be indistinctly present. The ventral surface of the nuchal plate is slightly depressed centrally without a conspicuous longitudinal median groove as in *Phyllolepis orvini* (Stensiö, 1934: 46), although a broad median depression may sometimes be present (e.g. holotype, Fig. 4A).

The median dorsal plate (MD) is broader than long with the posterolateral corners
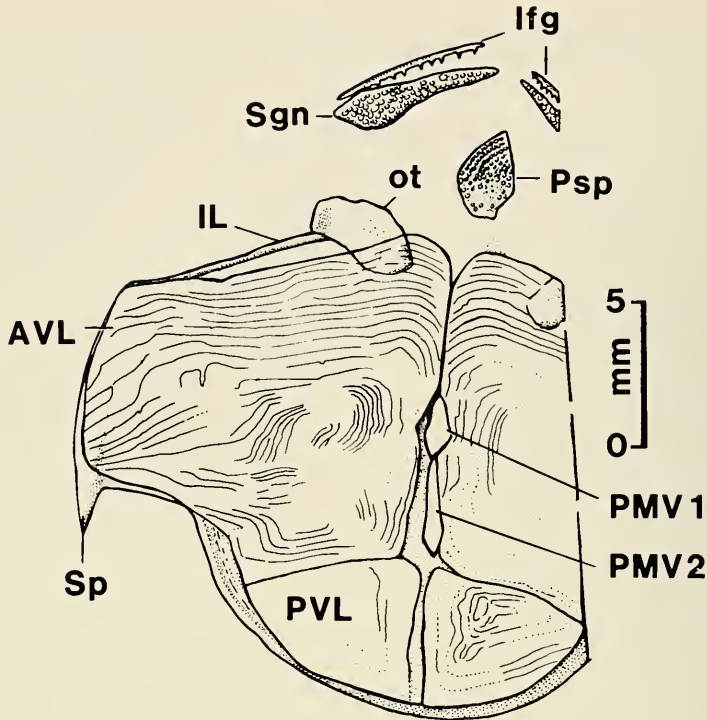
Fig. 6. *Austrophyllolepis ritchiei* gen. et sp. nov. Juvenile armour in ventral view showing the abnormal development of two median ventral plates. NMP 160726. AVL, anterior ventrolateral plate; Ifg, inferagnathal; IL, interolateral plate; ot, otolith; PMV1,2, posterior median ventral plates; Psp, parasphenoid; PVL, posterior ventrolateral plate; Sgn, supragnathal; Sp, spinal plate.

situated at approximately half the plate length. The anterior margin is straight with the anterolateral margin meeting at an angle of 110 degrees when undistorted. The ventral surface is smooth with a slightly thickened rim, lacking a median groove.

The anterior dorsolateral plate (ADL) is slightly shorter and broader than that of *Phyllolepis*. The anterior face of this plate has a broad flange for the PNu plate, typical of actinolepidoid euarthrodires. The ADL plate is slightly broader than long with the external ornamented surface having a B/L index ca 10 (Fig. 3**B, C**).

The anterior lateral plate (AL) is of similar shape to that of *Phyllolepis*. The proportion of the B:L of the mesial margin is from 85-100, with overall B/L index close to 57. The anteromesial angle is 120°.

The spinal plate (Sp) has small, broad lateral spines. About 25% of the spinal plate extends posterior to the AL plate.

The interolateral plate (IL) is very similar to that of *Phyllolepis orvini* (Stensiö, 1936: 42), differing slightly by the even curvature of the anterior margin. There is a well-defined ridge at the junction of the anterior concave face and the smoothly convex dorsal surface.

The anterior ventrolateral plate (AVL) of *Austrophyllolepis* is characterized by the posteromesial notch for the PMV plate (Figs 5, 7). In *A. ritchiei* there is an anteromesial angle of 80° with a posteromesial angle (extrapolating the margins at the notch for the posterior median ventral plate) of 64°. The lateral margin which meets the spinal plate
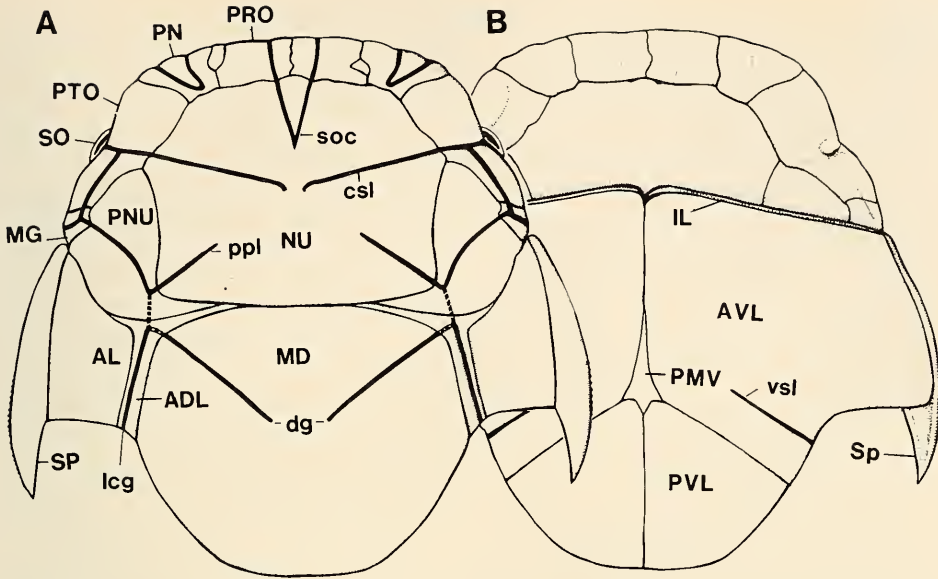
Fig. 7. *Austrophyllolepis ritchiei* gen. et sp. nov. Restoration of the dermal armour in **A**, dorsal and **B**, ventral views. ADL, anterior dorsolateral plate; AL, anterior lateral plate; AVL, anterior ventrolateral plate; csl, central sensory line canal; dg, dorsal sensory line canal; IL, interolateral plate; lcg, main lateral line canal; MD, median dorsal plate; Mg, marginal plate; Nu, nuchal plate; pmc, postmarginal sensory line canal; PMV, posterior median ventral plate; PN, postnasal plate; PNu, paranuchal plate; ppl, posterior pit-line canal; PRO, preorbital plate; PTO, postorbital plate; PVL, posterior ventrolateral plate; SO, suborbital plate; Sp, spinal plate; vsl, ventral sensory line canal.

is approximately 55% of the plate length. The anterior division of the plate is the area from the anterior limit of the plate to the transverse line crossing the anterolateral corner, perpendicular to the mesial margin. The length of this region is approximately 10% of the plate length. Total B/L index for large AVL plates is ca 90 whereas for juveniles this may be ca 97.

The posterior ventrolateral plate (PVL) is broader than long for juveniles (NMP 160726 B/L index is 124) the mature B/L index is ca 78. The posterior division of the lateral margin is quite convex.

The posterior median ventral (PMV) plate is lanceolate with a B/L index ca 60. One juvenile specimen, NMP 160726, shows two median ventral plates between the AVL plates (Fig. 6). The posterior element is narrow and lanceolate in form like the PMV plate of mature individuals. The anterior element is proportionately broader and is situated midway between the mesial margins of the AVL plates which contact each other anterior to the median bones. This precludes the possibility of the anterior plate in NMP 160726 being an AMV plate homologous to that of *Phyllolepis woodwardi* or euarthrodires. It is probable that this is an abnormality as sometimes occurs in the fractionation of plates in *Bothriolepis canadensis* (Stensiö, 1948: 262).

Austrophyllolepis youngi sp. nov.
Fig 2A-**2**; 9-13; 16; 18A, **B**; 19A; 20; 21; 22, 25**B**.

Etymology: After Dr Gavin Young, Bureau of Mineral Resources, Canberra.
Material: Holotype NMP 160718, complete individual preserved as a mould of both
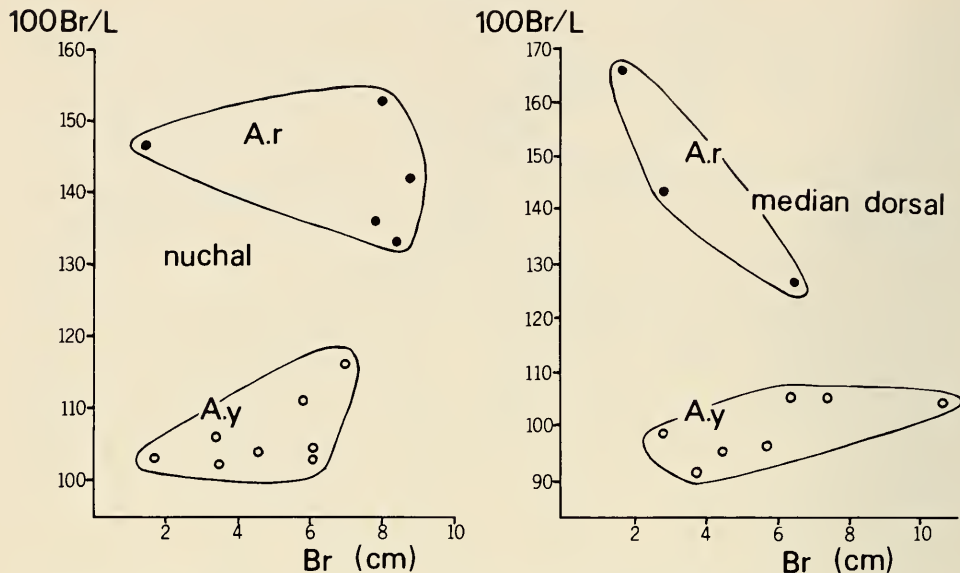
Fig. 8. Graphic representation of proportional differences between the nuchal and median dorsal plates of *Austrophyllolepis ritchiei* (A.r) and *A. youngi* (A.y) for all stages of growth. Vertical parameter is the breadth/length index, horizontal axis is plate breadth in centimetres.

dorsal and ventral surfaces (Figs 9, 10). Relatively complete individuals: NMP 160719, NMP 160720, NMP 160724, NMP 160725, NMP 160727, NMP 160730, NMP 160747, NMP 160749, NMP 160751, NMP 160752. NMP 160733, imperfect headshield. NMP 160739, portion of ventral surface. NMP 160740, imperfect ventral surface. NMP 160741, imperfect median dorsal plate. NMP 160746, imperfect ventral surface with tail and pelvic girdle. NMP 160756, imperfect headshield, portion of ventral surface of trunkshield.

Occurrence and age: From the main quarry and in the higher horizons above at Mt Howitt, in the lower mudstone of the Avon River Group exposed along the Bindaree section (Marsden, 1976).

Diagnosis: A slender *Austrophyllolepis* having a maximum mid-dorsal armour length up to 150 mm. The mature armour is longer than broad with a B/L index close to 80. Preorbital plate with an external B/L index from 90-140; paranuchal plate has an external B/L index from 45-52; nuchal plate has a B/L index from 100-112; median dorsal plate has a B/L index from 96-108. Anterior ventrolateral plate with an anteromesial angle around 70°, anterior division of plate around 23 % of the plate length, B/L index close to 70. Posterior ventrolateral plate with a B/L index from 67-72.

Remarks: Austrophyllolepis youngi is distinguished from *A. ritchiei* only by the proportions of the dermal armour (Figs 8, 25), specifically the preorbital, paranuchal, nuchal, median dorsal, anterior and posterior ventrolateral plates. Although the ornament appears to be more finely developed in some specimens of *A. youngi* relative to *A. ritchiei* it is not a distinguishing feature for the species as a whole. The hypothesis that these two forms are sexual dimorphs of the one species is difficult to test. Sexual dimorphism in placoderms is only positively known in ptyctodontids where the males possess dermal clasping elements (Miles, 1967a; Ørvig, 1960; Miles and Young, 1977). Where large numbers of placoderms in various growth stages are known (as for example the

Escuminac Bay *Bothriolepis canadensis*) armour proportions are apparently not dimorphic, although this question requires a detailed biometric survey. The unusual pelvic girdle of *Austrophyllolepis* shows similarities to the pelvic girdle of primitive male chondrichthyans, such as *Cobelodus* (Zangerl, 1981). Specimens which show the long propterygial element belong to both *A. ritchiei* (NMP 160750) and *A. youngi* (NMP 160732, 160746; Figs 21, 22) which precludes the possibility of these two forms being sexual dimorphs of the same species, although it is feasible that the few specimens displaying the pelvic girdle represent males of each species. Unfortunately there are too few specimens with the pelvic girdle preserved to demonstrate whether the propterygial element is really a clasping organ or an extension of the pelvic fin. *A. ritchiei* appears to be present at Freestone Creek without *A. youngi*, supporting the view that these are separate species, although further work on the Freestone Creek material is necessary to confirm this opinion. In view of the absence of claspers in most placoderms (excluding ptyctodontids) it is safer to accept the latter explanation.

Description: Characteristic features of individual plates for the genus *Austrophyllolepis* along with specific features of *A. ritchiei* were given above. The following description merely summarizes proportional differences for plates which can be distinguished from *A. ritchiei.*

The preorbital plate (PRO) is characteristically narrower than for *A. ritchiei*, and in the holotype (Figs 9, 10) shows a more tubercular ornament. The supraorbital canal appears to run closer to the mesial margins of the PRO plates at the Nu margin than in *A. ritchiei*. In juveniles such as NMP 160733 (Fig. 11**A, C**) these canals converge at the posteromesial corners of the PRO plates.

The postnasal plate (PN) has a slightly larger external posterior margin than for the previous species, the ratio of this margin over the anterior margin being close to 44 for *A. ritchiei* and from 50-57 for *A. youngi.*

The postorbital plate (PTO) is indistinguishable between the species, although some examples of *A. youngi* display a finer ornament (e.g. NMP 160718, Fig. 9; NMP 160724, Fig. 11**D**; NMP 160747, Fig. 11**B**).

Aside from the proportions given in the diagnosis the only distinguishing feature of the paranuchal plate (PNu) of *A. youngi* is the slightly more acute angle of the anterior apex (compare Figs 4**A** and 9**B**).

The nuchal plate (Nu) of *A. youngi* is distinctly narrower and tapers more posteriorly, and on some specimens lacking ornamentation on the flanks between the central sensory line canal and the posterior pit line canal (NMP 160718, Figs 9**A**, 10; NMP 160720, Fig. 11**B**; NMP 160724, Fig. 12**B**; NMP 160727).

The median dorsal plate (MD) of *A. youngi* may also show regions on the flanks devoid of ornament (NMP 160718, Figs 9**A**, 10, to a lesser extent NMP 160725) but not consistently (NMP 160747, Fig. 12**A**). In some specimens there is a median dorsal ridge present, although this may only be an artifact of preservation (e.g. NMP 160718, Fig. 9**A**; 160725, Fig. 12**B**).

The anterior dorsolateral (ADL), interolateral (IL) and anterior lateral (AL) plates of *A. youngi* are virtually indistinguishable from those of *A. ritchiei*. The spinal plates (Sp) of *A. youngi* project beyond the AL plate for up to 37% of their total length (Fig. 11**D**), significantly more than for *A. ritchiei.*

The anterior ventrolateral plate (AVL) of *A. youngi* is readily distinguished from that of *A. ritchiei* by the proportions and angles stated in the diagnosis.

The posterior ventrolateral plate (PVL) is narrower than for *A. ritchiei* with a B/L index from 60-72.
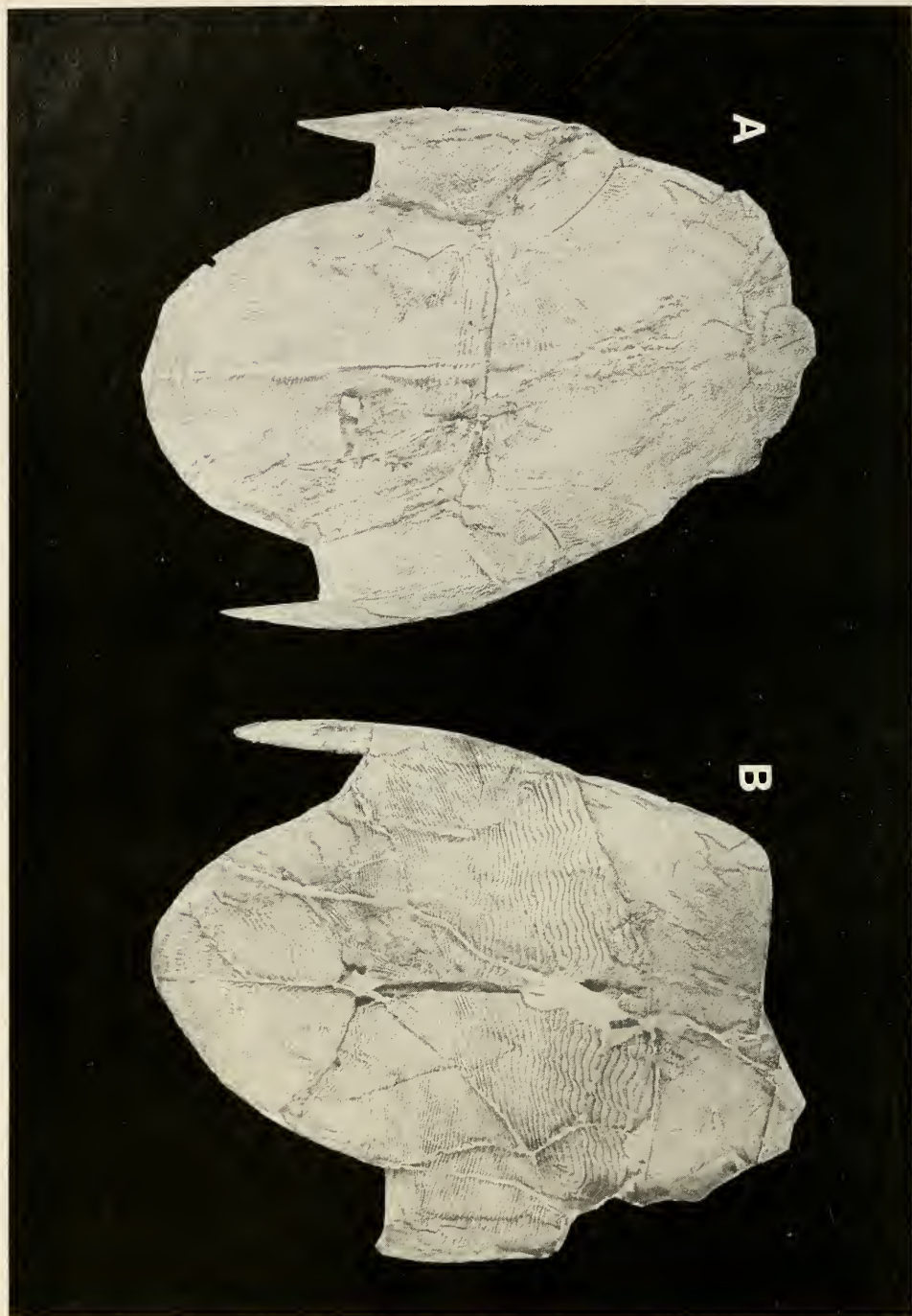
Fig. 9. Austrophyllolepis youngi gen. et sp. nov. Holotype, entire dermal armour in **A**, dorsal and **B**, ventral views. NMP 160718, latex cast whitened with ammonium chloride, natural size.
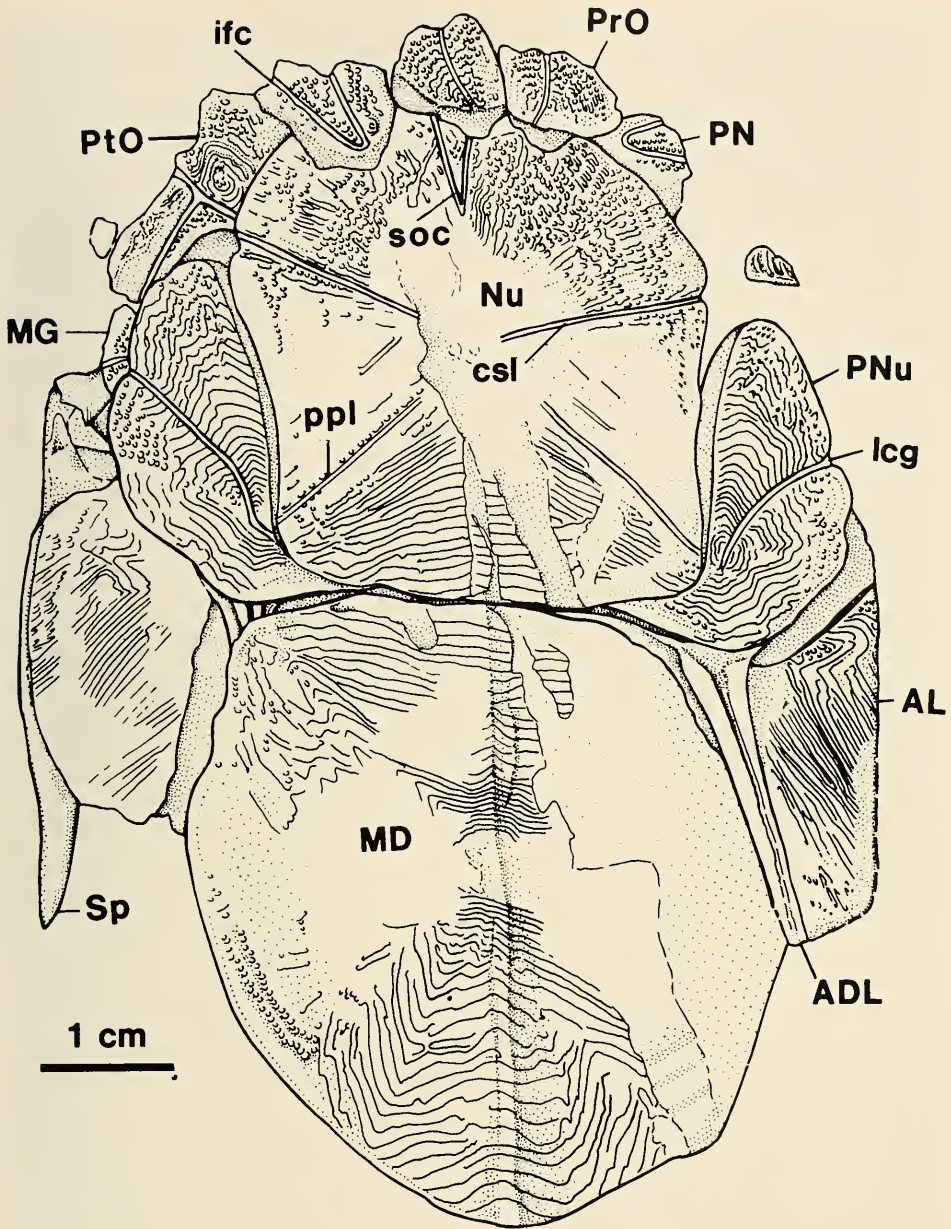
Fig. 10. Austrophyllolepis youngi gen. et sp. nov. Holotype armour in dorsal view, NMP 160718. Abbreviations as for Fig. 7.

NEW ANATOMICAL OBSERVATIONS

Headshield and Endocranium: The only observation worthy of note concerning the skull roof pattern of *Austrophyllolepis* is the infrequent presence of small plates between the PRO and PN plates (NMP 160721, NMP 160723; Figs 3A, 7A). These small plates probably result from fragmentation of larger adjacent plates.

The ventral surface of the headshield (Fig. 14) is characterized by the peripheral ridges and grooves which outline the dorsal surface of the endocranium, as in euarthrodires (Miles and Westoll, 1968) and antiarchs (Stensiö, 1948). The supraorbital vault (sov) is restricted to the anterior half of the PTO plate, thus differing from most placoderms where it extends onto the PRO. Posterior to the supraorbital vault on the PTO plate is a central thickening of bone (pr.ant) to which the small cheek plate (SO) firmly attaches. The posterior half of this plate bears a well-defined crista for the posterior postorbital process of the endocranium (pr.ppo). Lateral to this crista is a smooth region of bone which decreases in thickness near the margin. The extent of the postorbital process is clearly indicated by the ventral recess on the MG plate. The PNu plate possesses a short but well-defined paranuchal crista (cr.PNu) for the craniospinal process of the endocranium (pr.csp). The lateral line canal is sometimes discernible on the ventral surface by a low ridge (ri.lc). The anterior plates of the headshield are devoid of features on their ventral surfaces apart from the thickenings of bone below the laterosensory canals. The postethmoid region of the endocranium probably extended to the limit of the dermal exocranium, as suggested by the presence of many small pores at the anterior margin of the PRO and PN plates. As discussed above, the position of the rhinocapsular bone (rh, Fig. 15) was presumably directly anterior to the PRO plates, and anterolateral to the PN plates. This is the case for broad-shielded actinolepidoids such as *Aggeraspis* (Gross, 1962) and phlyctaenioids.such as *Gaspeaspis* (Pageau, 1969).

The form of the endocranium can be reconstructed from the features of the ventral surface of the skull roof described above (Figs 14B; 15B). The anterior postorbital process (pr.ant) is weakly developed as in most euarthrodires (e.g. *Dicksonosteus,* Goujet, 1975; *Buchanosteus,* Fig. 15C; after Young, 1979). The posterior postorbital process (pr.ppo) is well produced, as for all euarthrodires, although it cannot be determined whether there is a single process in this region or a bifid structure with a paravagal fossa. The cucullaris fossa (cuc.f) is long relative to the size of the endocranium, extending almost half the total length.

The endocranium of phyllolepids was undoubtedly cartilaginous as suggested by Stensiö (1936, 1969) and Denison (1978). No bone is present under the headshield of the Mt Howitt specimens, despite the delicate preservation of the gnathalia and parasphenoid. The absence of dermal bones normally associated with the rhinocapsular, such as the rostral and pineal plates, indicates that the snout consisted of a soft rostrum, more likely to be shorter and broader than in Stensiö's reconstruction (1963: fig. 3B).

In most of the *Austrophyllolepis* specimens with the ventral aspect of the headshield preserved there are two dense calcareous bodies situated close to the centre of the headshield oriented slightly anterolaterally, but symmetrical about the midline (Figs 4A, C; 9B; 11C, D; 12C; 14A; 15; 17; 18C; 20C). They are calcareous as they dissolve in weak hydrochloric acid, and have a similar mineralized appearance to the bone of the plates. In cross section they are compressed, flat dense bodies. Imperfect specimens indicate that they are not hollow, and compression of the anterior ventrolateral plates around these structures testifies to their solidity. There is no surface ornamentation although some specimens have transverse ribbing somewhat radially directed (e.g. NMP 160731, Fig. 18C; NMP 160737, Fig. 17). In life these structures were internal,
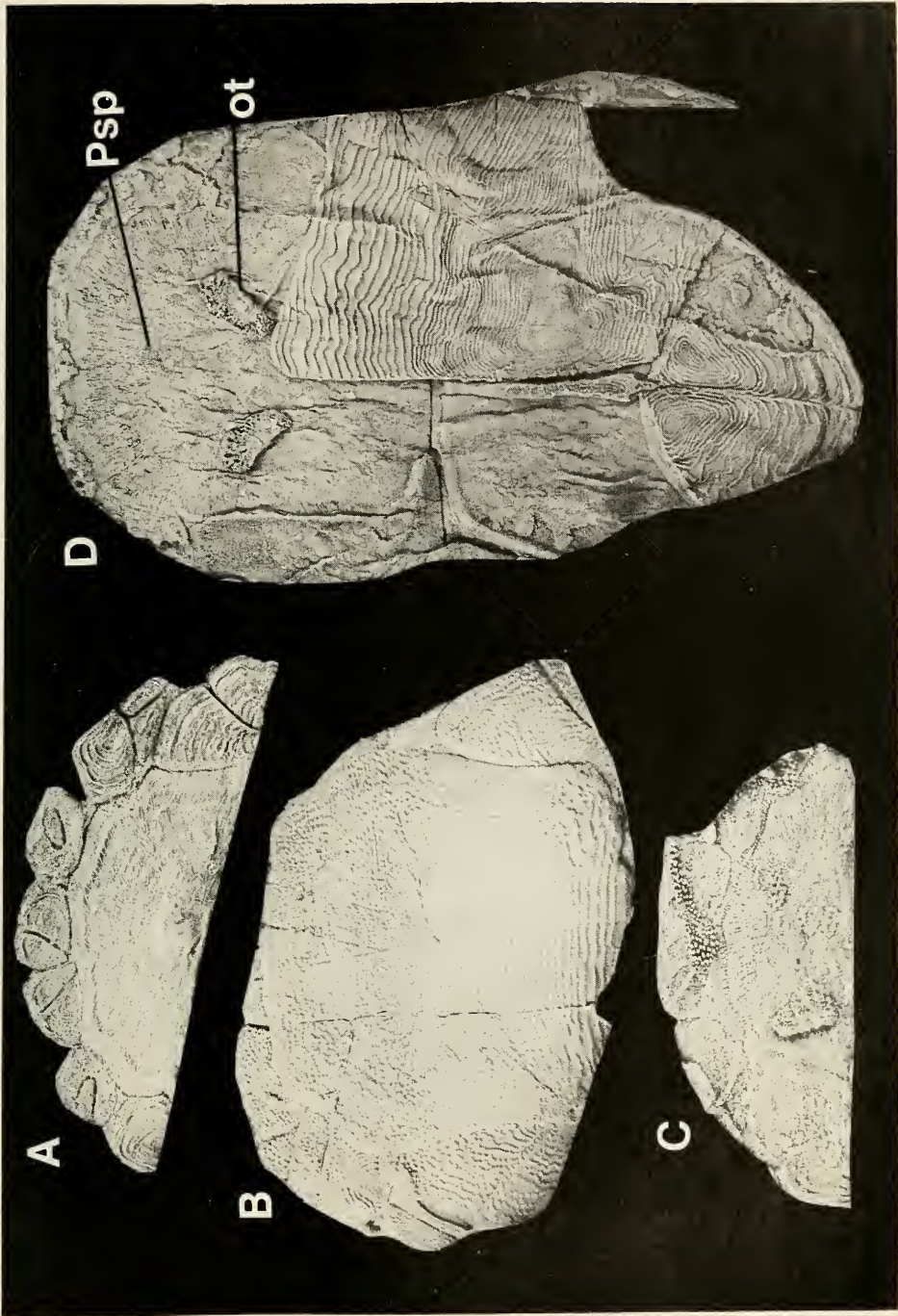
Fig. 11. Austrophyllolepis youngi gen. et´sp. nov. **A, C,** juvenile partial headshield in dorsal and ventral views, NMP 160733, × 2. **B,** slightly disrupted headshield in dorsal view, NMP 160720, natural size. **D,** ventral view of armour with otoliths (ot) and parasphenoid (Psp) preserved, NMP 160725, × 2. Latex casts whitened with ammonium chloride.
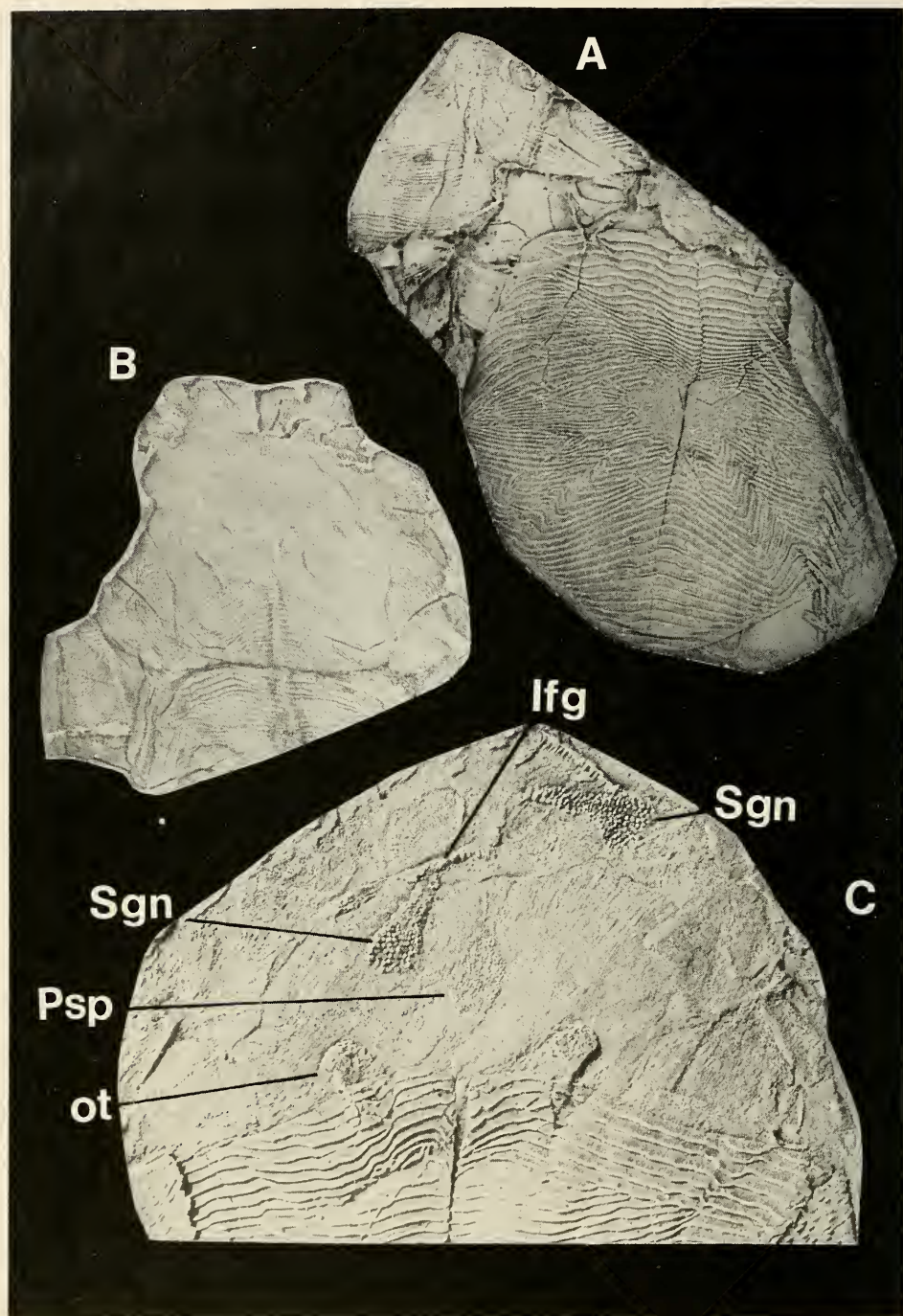
Fig. 12. *Austrophyllolepis youngi* gen. et sp. nov. **A,** imperfect armour in dorsal view, NMP 160747, natural size. **B,** headshield in dorsal view, NMP 160724, natural size. **C,** ventral aspect of headshield. NMP 160724. Ifg, inferagnathal; ot, otolith; Psp, parasphenoid; Sgn, supragnathal. Latex casts whitened with ammonium chloride.

and their position corresponds well to the estimated location of the saccular cavities in *Buchanosteus* (Young, 1979), *Kujdanowiaspis* (Stensiö, 1963), and other euarthrodires with dorsal saccular thickenings (e.g. *Stuertzaspis*, Fig. 15). I regard these calcareous bodies to be otoliths secreted inside the sacculus of each membranous labyrinth. Otoliths have not been previously recorded in placoderms although they are known in acanthodians (Miles, 1973) and primitive osteichthyans (Long, 1982a). Elasmobranchs secrete small particles together to form statoconia, allowing entry of the grains into the saccular and other cavities by the open endolymphatic ducts (Lowenstein, 1971). In *Austrophyllolepis* there is no indication of an open endolymphatic duct on the paranuchal plates as in other placoderms. This evidence supports the idea that *Austrophyllolepis,* and perhaps all phyllolepids, secreted statoliths rather than statoconia. The otoliths are present in the smallest specimen (NMP 160726; Figs 3, 6) where they are proportionately much larger than for mature individuals.

Jaws and parasphenoid: The gnathalia and parasphenoid are well preserved in several specimens of *Austrophyllolepis* (NMP 160719, NMP160720, NMP160721, NMP 160724, NMP 160725, NMP 160726, NMP 160727, NMP 160731, NMP 160733, NMP 160734, NMP 160737, NMP 160750). There is a single pair of upper tooth plates which are opposed by narrow inferognathals. The parasphenoid is a broad denticulated bone situated between the midpoint of the supragnathals.

The supragnathals (Sgn, Figs 4**A, C**; 5; 6; 11**C**; 12**C**; 14**B**; 16; 17; 18**B, C**; 20) are broadest posteriorly with narrow apices which almost meet in the midline. There are numerous conical teeth arranged in radial growth rows, the largest teeth being at the anterior division. The teeth are sharply pointed, not blunt tubercles, numbering up to 160 in mature individuals. Along the margin of the toothed surface of each Sgn is a narrow edentulous rim. The dorsal surface of the Sgn is known from one specimen only (NMP 160734), where it is smoothly concave at the broad posterior end.

Only one specimen shows the complete series of upper jaw ossifications present (NMP 160737, Fig. 17); presumably this is only developed at maturity. Posterior to the Sgn is a broader semicircular ossification which is firmly attached to a third element bearing a median thickening. This last component can be identified as the quadrate (quad, Fig. 17) because of its posterior position on the palatoquadrate and the median ridge, common on the quadrate of euarthrodires (Miles and Dennis, 1979; Miles, 1971; Dennis and Miles, 1979, 1980). The large flat central ossification between the quadrate and Sgn is the median division of the palatoquadrate or metapterygoid, primitively ossified in placoderms (Schaeffer, 1975; Goujet, 1975). In euarthrodires the jaw suspension is autostylic with attachment of the posterior end of the palatoquadrate complex to the dermal cheek bones. As the cheek of *Austrophyllolepis* was completely reduced save for one small bone, it is likely that the palatoquadrate complex was attached to the ventral surface of the endocranium, with articulation of the meckelian cartilage at the quadrate not being supported by a hyomandibular element. If an epihyal was present it must have been cartilaginous, and extended from the centre of the PTO plate posteriorly to the soft cheek region. Corresponding to the extreme dorsoventral compression of the phyllolepid body is the broad, flat metapterygoid for insertion of the adductor mandibulae.

The inferognathals (Ifg, Figs 4**A, C**; 5; 6; 12**C**; 16; 17; 18**B**; 20) bear teeth throughout their extent. There is one row of pointed teeth along the biting edge with a narrow cluster of teeth at the posterior end. In cross section the Ifg is divided into two laminae meeting at right angles: a dentigerous dorsal blade and a smooth vertical lamina which covered the anterior edge of the meckelian cartilage. The non-biting section of this cartilage which extended from the posterior of the Ifg to the quadrate was not ossified, even the articular was cartilaginous. This is an unusual condition because
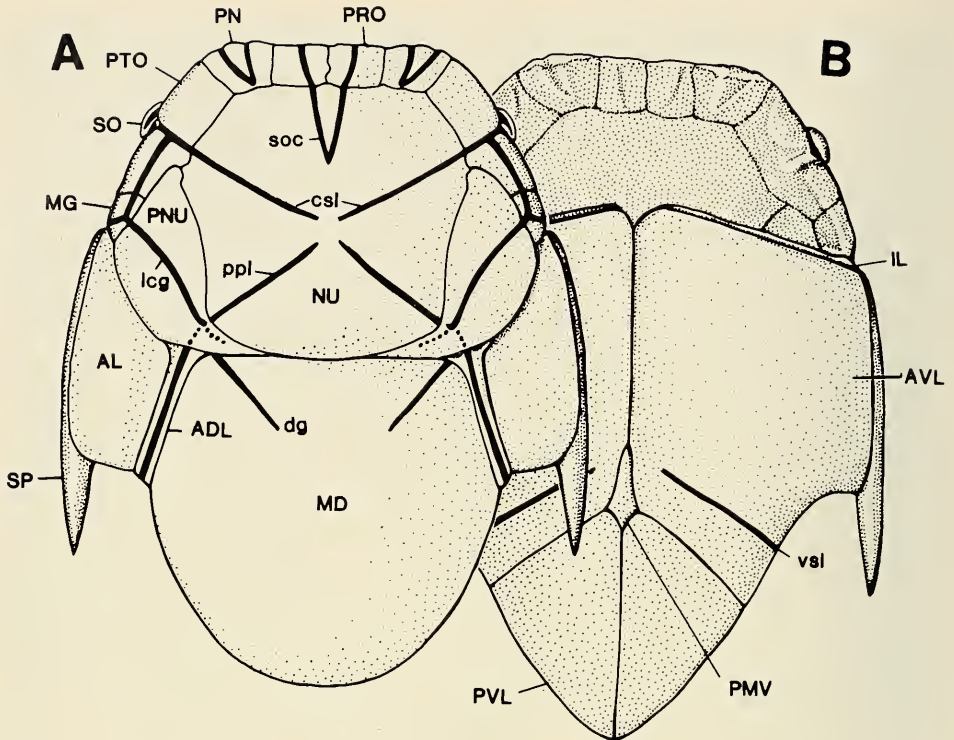
Fig. 13. *Austrophyllolepis youngi* gen. et sp. nov. Restored dermal armour in **A**, dorsal and **B**, ventral views. Abbreviations as for Fig. 7.

if the quadrate was ossified it would require equal strength in the articular region for maximum efficiency of the bite.

The parasphenoid (Psp, Figs 4**A**, **C**; 5; 6; 7**B**; 11**C**, **D**; 12**C**; 14**B**; 17; 18**C**; 20) is a broad bone with a subtriangular shape similar to that of *Buchanosteus* (Young, 1979). There is a broad edentulous margin around the central toothed area which encloses a small, paired buccohypophysial foramen (bhf), seen on the holotype of *A. ritchiei*. The anterior and lateral extensions of the margin are incised with radial striae in mature individuals, in juveniles there is no development of the smooth margin, only a toothed region. The lateral groove of the Psp is seen clearly as an indentation of the broad edentulous margin at the level of the buccohypophysial foramen. In this respect it is not like the Psp of *Buchanosteus* (Young, 1979) or higher euarthrodires such as coccosteomorphs (Miles and Dennis, 1979; Stensiö, 1969) which have well-developed lateral grooves invading the toothed centre of the bone, or occupying most of the ventral face of the bone. The Psp in phyllolepids was situated almost in the centre of the head, unlike most euarthrodires and the rhenanid *Kosoraspis* (Gross, 1931) which have the Psp anteriorly located. From this and the relative size of the gnathalia it can be deduced that the buccal cavity of phyllolepids was quite large.

Cheek: The cheek of *Austrophyllolepis* bears a single small bone (Figs 3**A**, **D**; 4**A**; 5; 7; 13; 14**A**; 16; 18**A**, **B**; 19) which firmly attached to the central bony process on the ventral surface of the PTO plate. It is preserved on few specimens (NMP 160719, NMP 160721, NMP 160722, NMP 160723, NMP 160737) but is always small and in-
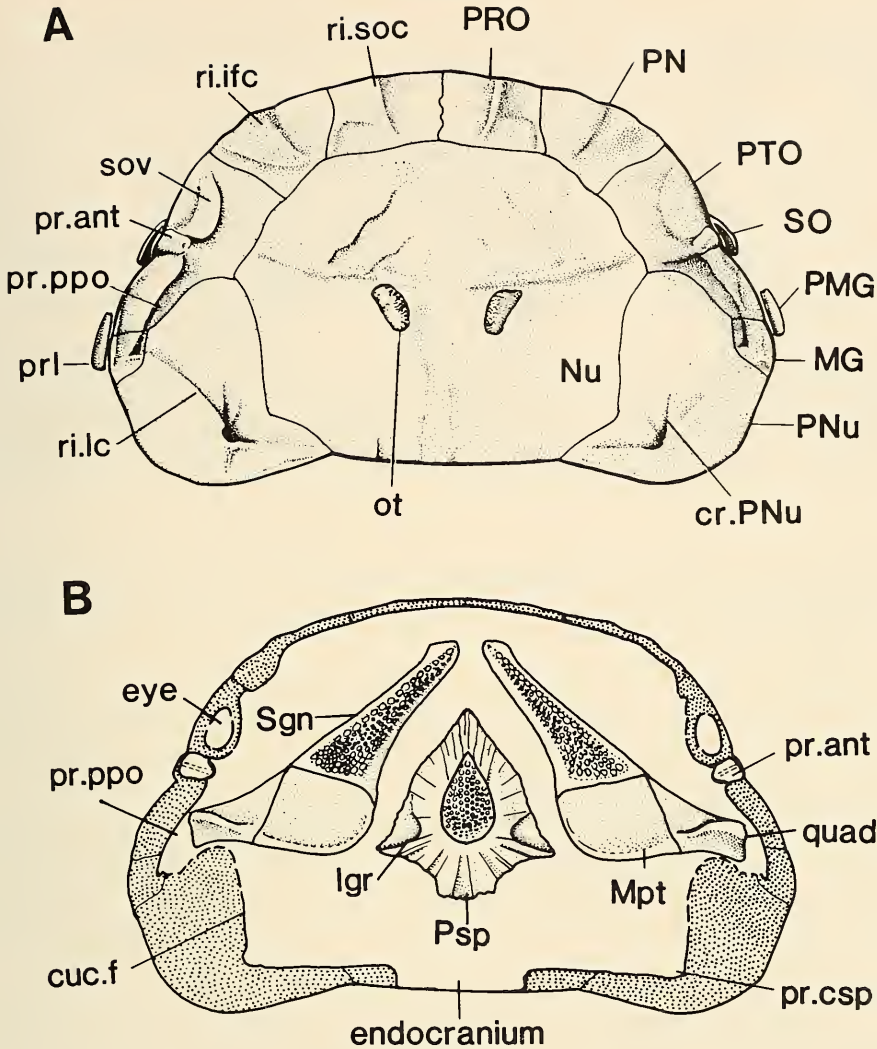
Fig. 14. **A**, restoration of the visceral surface of the headshield of *Austrophyllolepis ritchiei* gen. et sp. nov. **B**, reconstruction of the dorsal outline of the endocranium with gnathal bones and parasphenoid shown in position. cr.PNu, paranuchal crista; cuc.f; cucullaris fossa; lgr, lateral groove of parasphenoid; MG, marginal plate; Mpt, metapterygoid ossification of the palatoquadrate; Nu, nuchal plate; ot, otolith; PN, postnasal plate; PNu, paranuchal plate; pr.ant, anterior postorbital process of the endocranium; pr.csp, craniospinal process of the endocranium; prl, posterolateral corner of headshield; PRO, preorbital plate; pr.ppo, posterior postorbital process of the endocranium; Psp, parasphenoid, PTO, postorbital plate; ri.ifc, ridge below infraorbital canal; ri.lc, ridge below main lateral line canal; ri.soc, ridge below supraorbital sensory line canal; SO, suborbital plate; sov, supraorbital vault.

complete. It is difficult to homologize this bone with the suborbital (SO), post-suborbital (PSO) or submarginal (SM) plates of other placoderms because it lacks ornamentation, bears no distinct grooves for laterosensory lines and has a unique shape. The smooth surface on both sides of the bone is folded to form a double lamina with a large valley in between. It is oriented with the opening of the folded laminae on
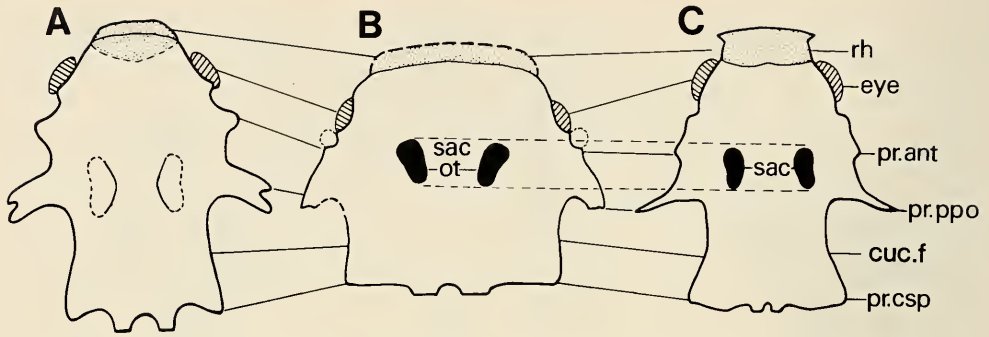
Fig. 15. Dorsal endocranial outlines of **A**, *Stuertzaspis*, (after Westoll & Miles, 1963) **B**, *Austrophyllolepis ritchiei* and **C**, *Buchanosteus* (after Young, 1979), showing the relative size of the saccular otoliths (sac ot) in *Austrophyllolepis* by comparison with the size and position of the saccular cavities (sac) of *Buchanosteus*, and their inferred position in *Stuertzaspis*. Homology of the endocranial processes is shown in relation to orbital position. Rhinocapsular regions (rh) stippled (conjectural for *Austrophyllolepis*). Abbreviations as for Fig. 14.

the dorsal side and the convex lateral side facing out from the notch in the PTO plate where the infraorbital sensory line departs the exocranium. This sensory line appears to run into the valley between the laminae of the cheek bone where the infraorbital sensory line of most placoderms divides to send a supraoral line ventrally. If this hypothesis is plausible then the cheek bone of *Austrophyllolepis* is probably a modified SO plate. The SO plate in euarthrodires and the palaeacanthaspidoid *Romundina* is situated opposite the PTO plate where the infraorbital sensory line leaves the skull roof. The PSO and SM plates are absent in phyllolepids.

An alternative explanation for the cheek bone in phyllolepids is that it could be a unique development which housed an electric organ. In Torpediformes such electric organs are located in the same position facing dorsally to stun prey swimming above the fish (Bennet, 1971). The internal area of the phyllolepid cheek bone housed the sensory line plexus where the infraorbital line probably divided into supraoral and infraorbital lines.

Postmarginal plate: In two specimens (NMP 160720, NMP 160723; Figs 19**B**, **C**; 20) there is a small bone adjacent to the MG plate. This bone is unornamented and lacks a laterosensory groove. In NMP 160720 it is clearly overlapped by the MG plate, as seen in ventral view (Fig. 20). It is possible that this bone is a small postmarginal plate (PMG) which was loosely attached to the cheek in phyllolepids. However as it is only seen on two specimens, and was not observed in the East Greenland material it cannot be confidently identified as a PMG plate. In NMP 160723 it is possible that the bone adjacent to the MG plate is actually a piece of the right IL plate which has been displaced.

Tail and axial skeleton: The tail of *Austrophyllolepis* is almost entirely preserved on NMP 160750, NMP 160751 and NMP 160732 (Fig. 22A), with sections of the tail preserved in NMP 160728, NMP 160746 (Figs 21; 22**B**), NMP 160752, NMP 160754 and NMP 160757. As in other placoderms perichondrally ossified neural and haemal arches surround the cartilaginous notochord (Miles and Westoll, 1968; Dennis and Miles, 1981). There is no submedian dorsal plate nor anal interseptal plate ossification. At least 40 vertebrae were present. The orientation of the tail elements is taken from the accompanying dermal armour. In NMP 160732 the armour is preserved in ventral view with the rows of Y-shaped arches having their notochordal saddles facing ven-
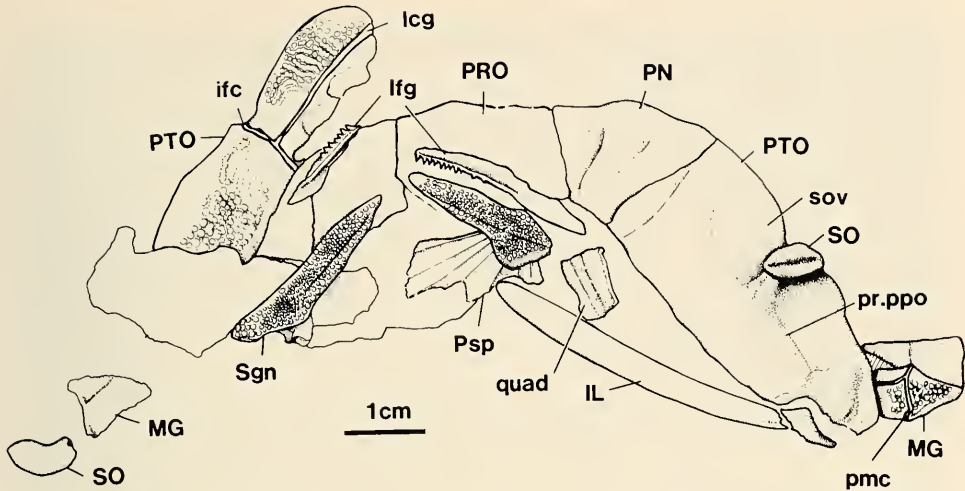
Fig. 16. *Austrophyllolepis youngi* gen. et sp. nov., ventral surface of slightly disrupted headshield. NMP 160719 (see also Fig. 18B). ifc, infraorbital sensory canal; Ifg, inferagnathal; IL, interolateral plate; lcg, main lateral line canal; MG, marginal plate; pmc, postmarginal sensory line canal; PN, postnasal plate; PRO, preorbital plate; pr.ppo, groove for posterior postorbital process of the endocranium; Psp, parasphenoid; PTO, postorbital plate; quad, quadrate; Sgn, supragnathal; SO, suborbital plate; sov, supraorbital vault.

trally, indicating that these were the haemal arches. The neural arches are paired, smaller elements which lie disrupted between the ordered rows of haemal arches.

The neural arches (neur) bear prominent anterior zygapophyses with lateral grooves on the neural spines for receiving the zygapophyses of the preceding vertebra. The saddle for the notochord is a strongly splayed cone of thin bone (n.gr). A slightly constricted neck joins the saddle to the neural arch. The neural arch elements do not vary much throughout their extent, unlike those of *Coccosteus* (Miles and Westoll, 1968) or *Ctenurella* (Ørvig, 1962).

The haemal arches (hae) comprise fused halves which meet to form a Y-shaped structure with a median groove (mg) in the confluence. The haemal spines are long, slightly compressed tubes with flared distal ends when they meet fin supports.

A cluster of additional perichondral tubes close to the dermal armour in NMP 160732 and NMP 160746 possibly represents the fin supports for a short dorsal fin behind the trunkshield. As a single dorsal fin is present on most placoderms (Denison, 1978) I have restored one on *Austrophyllolepis* (Fig. 23).

Pelvic girdle: The pelvic girdle is well preserved in NMP 160746 (Figs 19; 20B) and NMP 160750. It is situated immediately behind the trunkshield, and consists of two large perichondral ossifications: a broad basal pelvic plate (pel.b) and a slender propterygial element (pro). The basal plate is broadest at the proximal end where it appears to contact the PVL plate. The narrow posterior margin has a thickened articulation area for the propterygium. The lateral side of the basal plate has a distinct convex division separated in NMP 160746 from the broad proximal end by a concave anterior division. The convex division of the lateral margin bears short grooves (art) denoting serial divisions for articulation of cartilaginous pelvic fin ray elements. The anterior end of the propterygium is broader than the posterior end and has a large fossa for muscle attachment. The shaft of the propterygium narrows at the centre then expands slightly at the posterior end.
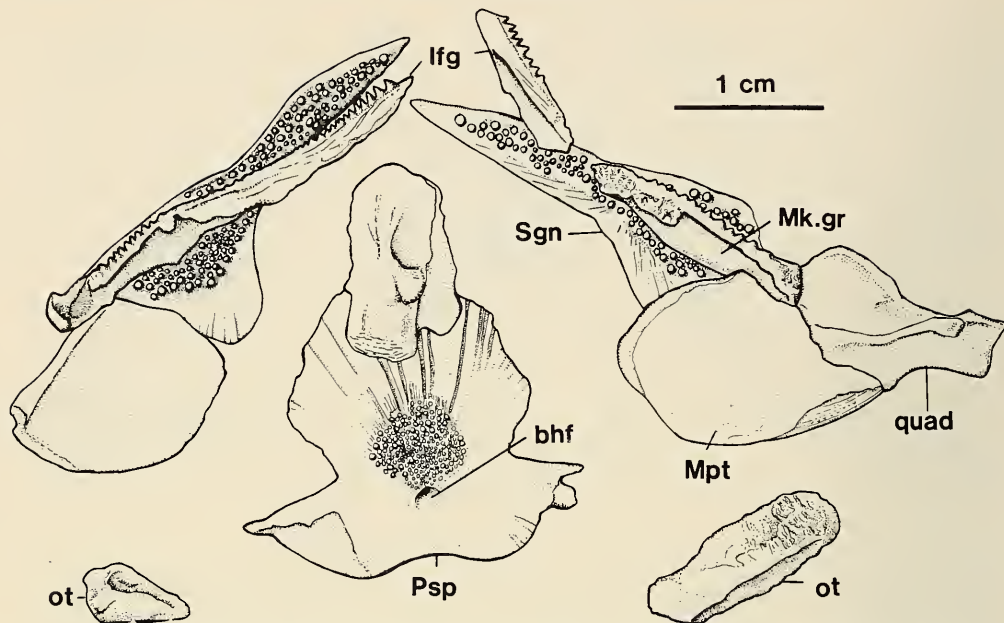
Fig. 17. Austrophyllolepis ritchiei gen. et sp. nov. Large individual showing the complete ossification series of the palatoquadrate, NMP 160737. bhf, buccohypophysial foramen; Ifg, inferagnathals; Mk.gr, groove for Meckel's cartilage; Mpt, metapterygoid; ot, otolith; Psp, parasphenoid; Sgn, supragnathal.

The pelvic girdle of *Austrophyllolepis* shows some resemblance to the male clasping organs of primitive chondrichthyans, particularly *Cobelodus* (Zangerl, 1981). As the long propterygial element of *Austrophyllolepis* is found in both species there is no case for sexual dimorphism producing the two varieties, yet it is feasible that sexual dimorphism may have occurred in both species but because there are too few specimens showing the pelvic girdle a female condition has not been observed.

COMPARATIVE ANATOMY OF PHYLLOLEPID FEATURES

Current hypotheses of placoderm interrelationships place the phyllolepids as the sister group to euarthrodires plus antiarchs (Miles and Young, 1977; Denison, 1978), as the sister group to antiarchs, euarthrodires and *Wuttagoonaspis* (Young, 1980) or as the sister group to euarthrodires (Goujet, 1984). As previous workers have taken only the form and arrangement of the armour into consideration, it is necessary to review the phylogenetic position of phyllolepids in the light of the new data provided by both *Austrophyllolepis* and *Placolepis*.

Headshield: One of the characteristic features of the phyllolepid headshield is the large Nu plate, or alternatively, if process is not invoked, undifferentiated Nu and Ce plates. A combined centronuchal plate is also known in *Wuttagoonaspis* (Ritchie, 1973), *Antarctaspis* (White, 1968; interpretation by Denison, 1978) and in an undescribed actinolepid euarthrodire from Severnaya Zemlya (Dr D. Goujet, pers. comm.). The potential for combining the Ce and Nu plates, or the loss of the Ce plates is restricted to phyllolepids, *Wuttagoonaspis* and some actinolepidoids.

A single pair of PNu plates is a synapomorphy uniting euarthrodires, antiarchs and phyllolepids according to Miles and Young (1977), and Young (1980), assuming that two pairs of PNu plates are primitive for placoderms. A single pair of large PNu
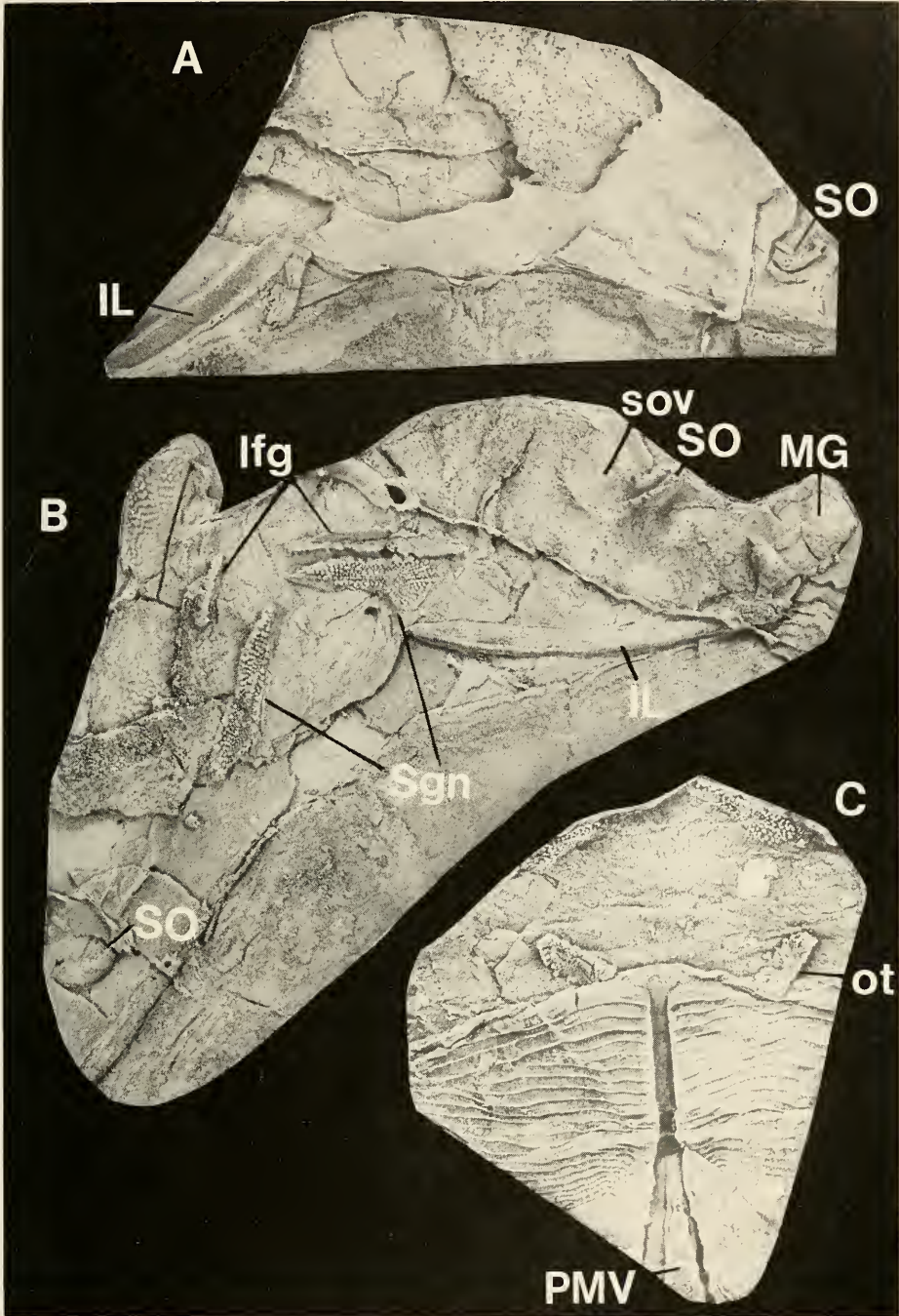
Fig. 18. **A, B.** *Austrophyllolepis youngi* gen. et sp. nov. Imperfect headshield in dorsal (**A**) and ventral (**B**) aspects, NMP 160719, natural size (see also Fig. 16). **C.** *Austrophyllolepis ritchiei* gen. et sp. nov. ventral aspect of juvenile, NMP 160731, × 2. Ifg, inferagnathal; IL, interolateral plate; Mg, marginal plate; ot, otolith; PMV, posterior median ventral plate; SO, suborbital plate; sov, supraorbital vault.
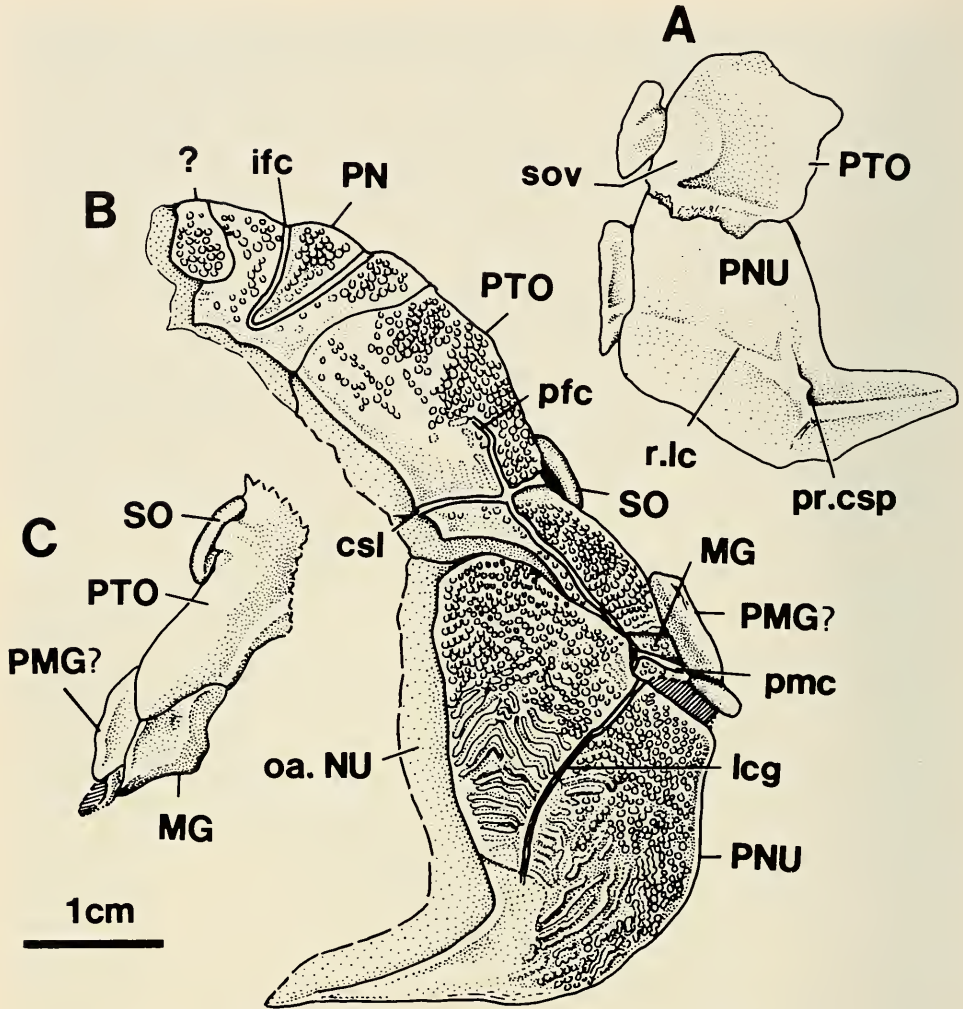
Fig. 19. **A.** *Austrophyllolepis youngi* gen. et sp. nov., visceral aspect of left side of headshield, NMP 160730. **B,** **C.** *Austrophyllolepis ritchiei* gen. et sp. nov., right side of headshield showing possible postmarginal plate, NMP 160723. csl, central sensory line canal; ifc, infraorbital sensory line canal; lcg, main lateral line canal; Mg, marginal plate; oa.Nu, area overlapped by nuchal plate; pmc, postmarginal sensory line canal; PMG, postmarginal plate?; pfc, profundus sensory line canal; PN, postnasal plate; PNu, paranuchal plate; pr.csp, craniospinal process ridge; PTO, postorbital plate; ri.lc, ridge underneath the lateral line canal; SO, suborbital plate; sov, supraorbital vault.

plates (covering most of the lateral occipital region of the skull roof) is a feature of phyllolepids and euarthrodires. Goujet (1984) uses the junction of the main lateral line canal with the posterior pit-line and occipital line of the PNu plate as a synapomorphy of phyllolepids and euarthrodires, presumably inferring the presence of an occipital pit line from the specimens of *Phyllolepis orvini* illustrated by Stensiö (1936: pl. 4, fig. 1; there appears to be a transverse extension of the main lateral line canal). If an occipital line was present in phyllolepids it would have transversed the neck superficially.

Paired PRO plates in mesial contact are found in ptyctodonts, some

petalichthyids, the palaeacanthaspidoid *Kimaspis* (Mark-Kurik, 1973), the rhenanid *Brindabellaspis* (Young, 1980), most euarthrodires, and most phyllolepids (in *Phyllolepis orvini* they are separated). However, only in one actinolepidoid, *Actinolepis* (Mark-Kurik, 1973) and phyllolepids do the PRO plates not form part of the orbital margin, thus exhibiting a degree of variability not seen by other placoderms. *Actinolepis* and phyllolepids have the orbit confined to the PTO plate (Fig. 1).

Having a PTO plate considerably larger than the MG plate is a characteristic feature of phyllolepids and some primitive euarthrodires (most conspicuous in *Anarthraspis, Simblaspis, Proaethaspis, Baringaspis, Antarctaspis* (Denison, 1978), and in *Wuttagoonaspis* (Ritchie, 1973)). Because several advanced brachythoracid characters separate *Pholidosteus* from actinolepidoids (Young, 1981b; Dennis and Miles, 1983), its large PTO is considered to be a parallelism. The MG plates of ptyctodontids, palaeacanthaspidoids, petalichthyids and most euarthrodires are relatively large, sometimes as large as the Ce or PNu plates, and this is here taken as the plesiomorphous placoderm condition. Only on phyllolepids, *Antarctaspis* and *Wuttagoonaspis* is the MG plate exceptionally small.

PMG plates are found in euarthrodires, antiarchs and possibly phyllolepids. In primitive antiarchs the PMG is large (Zhang Guorui, 1978) becoming smaller in later forms. In primitive euarthrodires the PMG is relatively large in some taxa (actinolepidoids: *Kujdanowiaspis, Baringaspis, Proaethaspis;* phlyctaenioids: *Phlyctaenius, Groenlandaspis*, Denison, 1978), and proportionately smaller on others (*Simblaspis, Aethaspis;* Denison, 1978). In higher euarthrodires the PMG plate is universally diminished, particularly so in *Bungartius* and *Tafilalichthys*. In *Synauchenia* the PMG and SM plates are combined into one small element. Diminution of PMG size is associated with the change of position from the posterolateral corner of the skull roof to the upper part of the cheek complex. The cheek of higher euarthrodires is fixed firmly to the rest of the exocranium (Denison, 1978; Miles and Dennis, 1979). In phyllolepids the reduction or loss of the PMG plate is probably a parallelism with that of the higher euarthrodires which follow the trend of reduction of the whole dermal cheek complex. In phlyctaenioids and some actinolepidoids the PMG plate is almost completely covered by the SM plate (Goujet, 1972; 1975), and further reduction of the PMG plate would not be unusual if this trend continued in association with other modifications of the cheek.

The ventral surface of the headshield in antiarchs, euarthrodires and phyllolepids is characterized by depressions and ridges for the dorsal surface of the endocranium. In ptyctodontids and presumably petalichthyids the ventral surface of the skull roof is relatively featureless apart from the tubes for the laterosensory nerves (Miles and Young, 1977: fig. 16; Young, 1978: fig. 4; Stensiö, 1969). In *Romundina* and *Brindabellaspis* there is a combination of ridges on the peripheral dermal bones along with large pipe-like tubes for the laterosensory line nerves (Ørvig, 1975; Young, 1980). The development of dermal bone supporting the optic capsules is quite different in the various placoderm groups. In *Brindabellaspis, Romundina,* and *Macropetalichthys* there is no dermal bone rim for the optic capsules, only a recessed area on the lateral endocranial wall. In ptyctodontids there is a thickened rim for the optic capsules on the PRO, PTO and MG plates (Miles and Young, 1977). An extensive dermal thickening above the eyeball is therefore restricted to phyllolepids and euarthrodires, with the development of an extensive ventrally projecting lamina behind the eyeball being a synapomorphy of higher euarthrodires (Dennis and Miles, 1983).

Autapomorphous features of the phyllolepid headshield are: a large PN plate contacting the centronuchal area and separating the PRO and PTO plates; no orbital notches in the headshield; no dermal bones of the snout (rostral and pineal plates); no
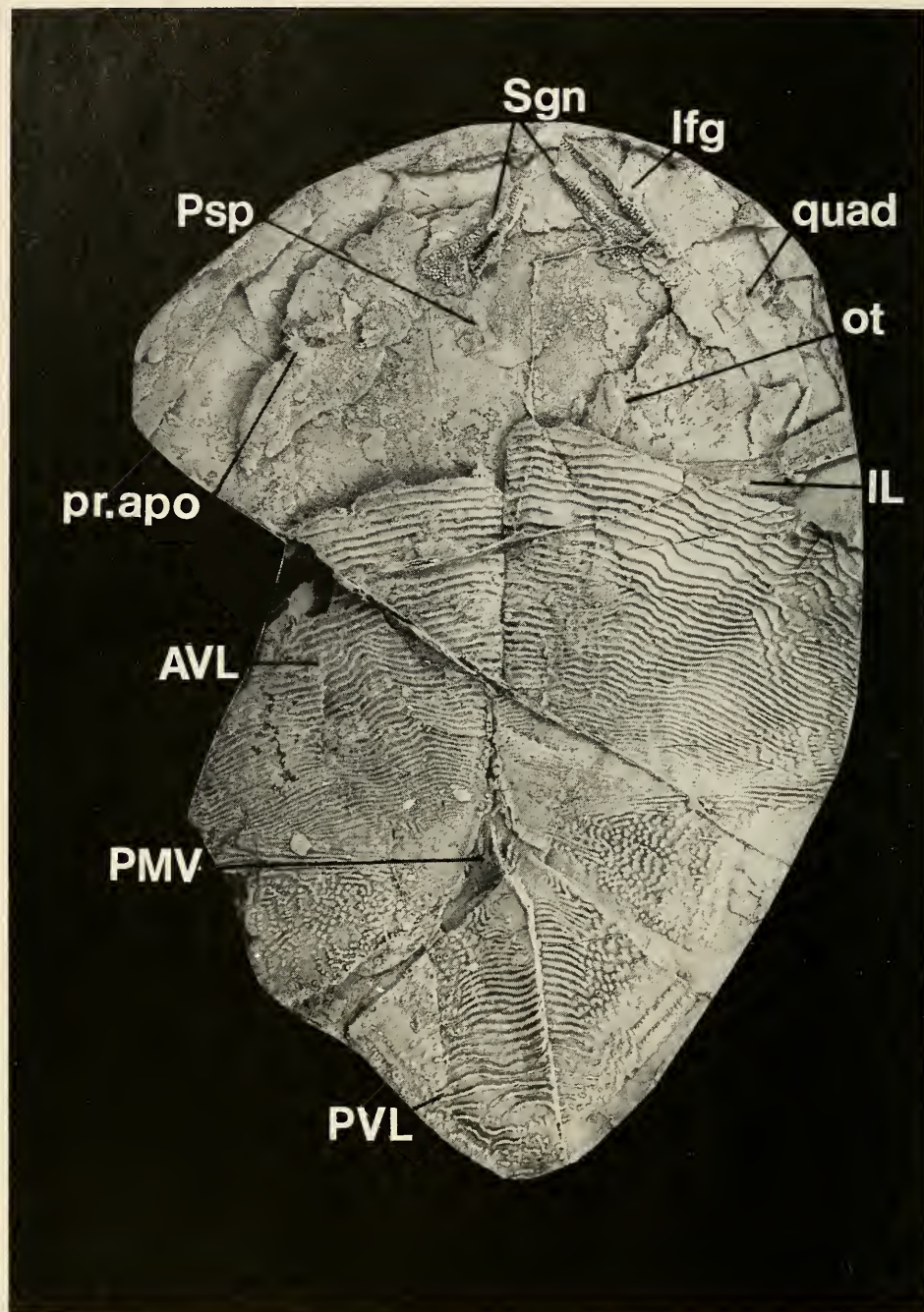
Fig. 20. Austrophyllolepis youngi gen. et sp. nov., ventral aspect of nearly entire individual, NMP 160720, natural size. AVL, anterior ventrolateral plate; Ifg, inferagnathal; IL, interolateral plate; ot, otolith; PMV, posterior median ventral plate; pr.apo, bony extension to the anterior postorbital process; Psp, parasphenoid; PVL, posterior ventrolateral plate; quad, quadrate; Sgn, supragnathal.

PSO and SM plates with extreme modification of the SO plate; and a completely flat exocranium which is proportionately broader than that of other placoderms.

Endocranium: Recent works since the monographs of Stensiö (1963, 1969) provide new data on the endocrania of placoderms (Goujet, 1975; Ørvig, 1975; Young, 1978, 1979, 1980) and permit more confident use of endocranial features in phylogenetic discussion. The endocranium of most placoderms was perichondrally ossified, but in phyllolepids and antiarchs it was presumably cartilaginous (also see comments in V. T. Young, 1983 regarding *Phlyctaenius*), and in ptyctodontids it was only partially ossified (Miles and Young, 1977). It follows that a well-ossified endocranium is the plesiomorphic condition for placoderms, secondary reduction of bone being a specialization of higher groups.

In phyllolepids and euarthrodires the endocranium has well-developed posterior postorbital processes, and a relatively large cucullaris fossa. The posterior postorbital processes are well produced in chondrichthyans, acanthodians and palaeoniscoids and it may be argued that these are a primitive gnathostome character (Schaeffer, 1981: 49). However in all recent schemes of placoderm interrelationships the euarthrodires are placed as a relatively derived group by comparison with petalichthyids, rhenanids (palaeacanthaspidoids and gemuendinaspidoids) and ptyctodontids. It follows that the absence of well-developed posterior postorbital processes in these primitive placoderm groups cannot be regarded as a synapomorphy of these groups on the grounds of character analyses put forward by several workers. I consider the well-developed posterior postorbital processes of euarthrodires and phyllolepids as a synapomorphy of these two relatively advanced placoderm groups, the distinction being that in these groups the posterior postorbital processes are more extended laterally than in any other placoderm group. Amongst the primitive placoderm groups these processes are perhaps best developed in *Romundina* (Ørvig, 1975; pls 1-3), and it is not unlikely that this represents the primitive placoderm condition for this character. Secondary extension (euarthrodires and phyllolepids) and reduction (other placoderms; except possibly antiarchs) of this endocranial ·process probably relate to differing placoderm feeding mechanisms and changes in the suspensorial framework (comments in Schaeffer, 1975, 1981; Miles 1967b, 1969; Young, 1980). The large cucullaris fossa of euarthrodires and phyllolepids is another synapomorphy of these groups related to the larger attachment area for the branchial constrictor and cucullaris muscles (Miles, 1967b). It is not known from the pattern on the ventral surface of the headshield of phyllolepids if the posterior postorbital process was bifid with a separate paravagal fossa.

Although the separation of the rhinocapsular from the postethmoid division of the endocranium is also seen in palaeacanthaspidoids (*Romundina*, Ørvig, 1975) and possibly in petalichthyids (*Macropetalichthys,* Stensiö, 1969: fig. 22), it is only in euarthrodires that the dermal exocranium shows two clear divisions which reflect the condition of the underlying endocranium. The separate terminal rhinocapsular of primitive euarthrodires, and presumably phyllolepids, is not seen on any other gnathostome group (De Beer, 1937), and could be regarded as a synapomorphy of these groups later modified in separate euarthrodire lineages. An example of this is the way dermal bones of the snout are fused to the rest of the exocranium, as is the condition in some phlyctaenaspids and most brachythoracids (Denison, 1978). I therefore regard this condition, viz., the dermal bones of the snout not fused to the rest of the exocranium leaving the rhinocapsular separate from the rest of the endocranium, as a synapomorphy of primitive euarthrodires and phyllolepids. This interpretation is more parsimonious than arguing monophyly for all euarthrodires with a separate rostral capsule (e.g. certain actinolepidoids and *Buchanosteus*).
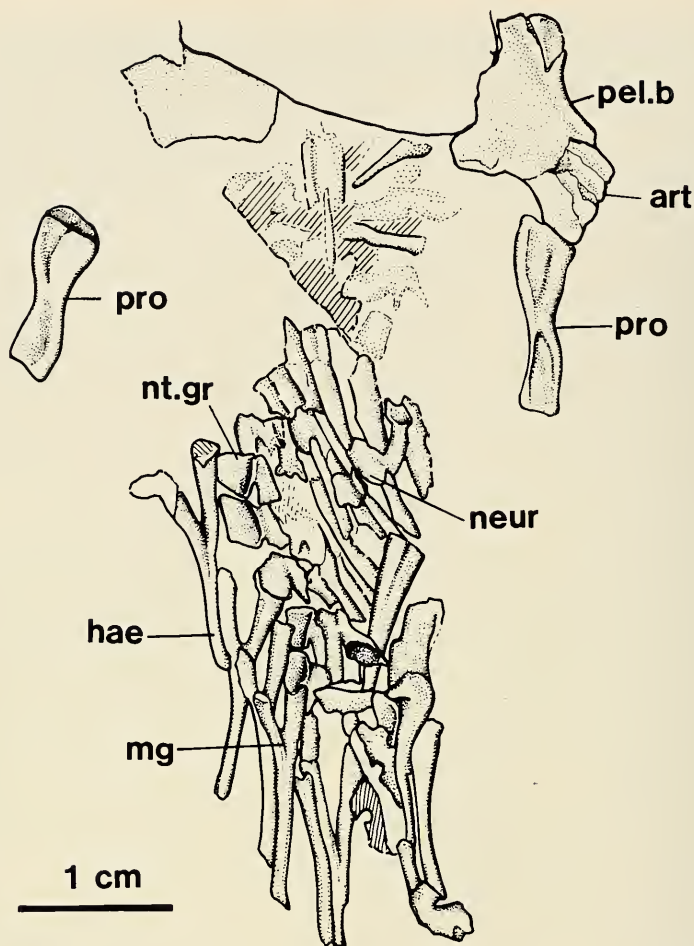
Fig. 21. *Austrophyllolepis youngi* gen. et sp. nov., pelvic girdle preserved in dorsal view, NMP 160746 (see also Fig. 22B). hae, haemal arch; mg, median groove on haemal arch; neur, neural arch; nt.gr, notochordal saddle on neural arch; pel.b, basal pelvic plate; pro, propterygial element of pelvic girdle.

    Autapomorphous features of the phyllolepid endocranium are the internally secreted otoliths in the saccular cavities, and possibly the ossified extension to the anterior postorbital process on the ventral surface of the postorbital plate.

Jaws and Parasphenoid: The jaws and parasphenoid of placoderms are widely known for advanced euarthrodires (Stensiö, 1969: figs 140-142; Miles, 1971: figs 56-61; Miles and Dennis, 1979; Dennis and Miles, 1979, 1980, 1981, 1982, 1983) but otherwise known only in the phlyctaenioids *Dicksonosteus* (Goujet, 1975) and *Groenlandaspis* (Dr A. Ritchie, pers. comm.), the actinolepidoid *Kujdanowiaspis* (Stensiö, 1963: pl. 62) and possibly actinolepidoid gnathals from America (Denison, 1958). The jaws are known in antiarchs (Stensiö, 1948; Hemmings, 1978), gemuendinaspids (Gross, 1963) and ptyctodontids (Ørvig, 1962; Miles and Young, 1977) but are unknown in petalichthyids and palaeacanthaspidoids. Outside of euarthrodires and phyllolepids, the parasphenoid is only known in the palaeacanthaspidoid *Kosoraspis* (Gross, 1959)
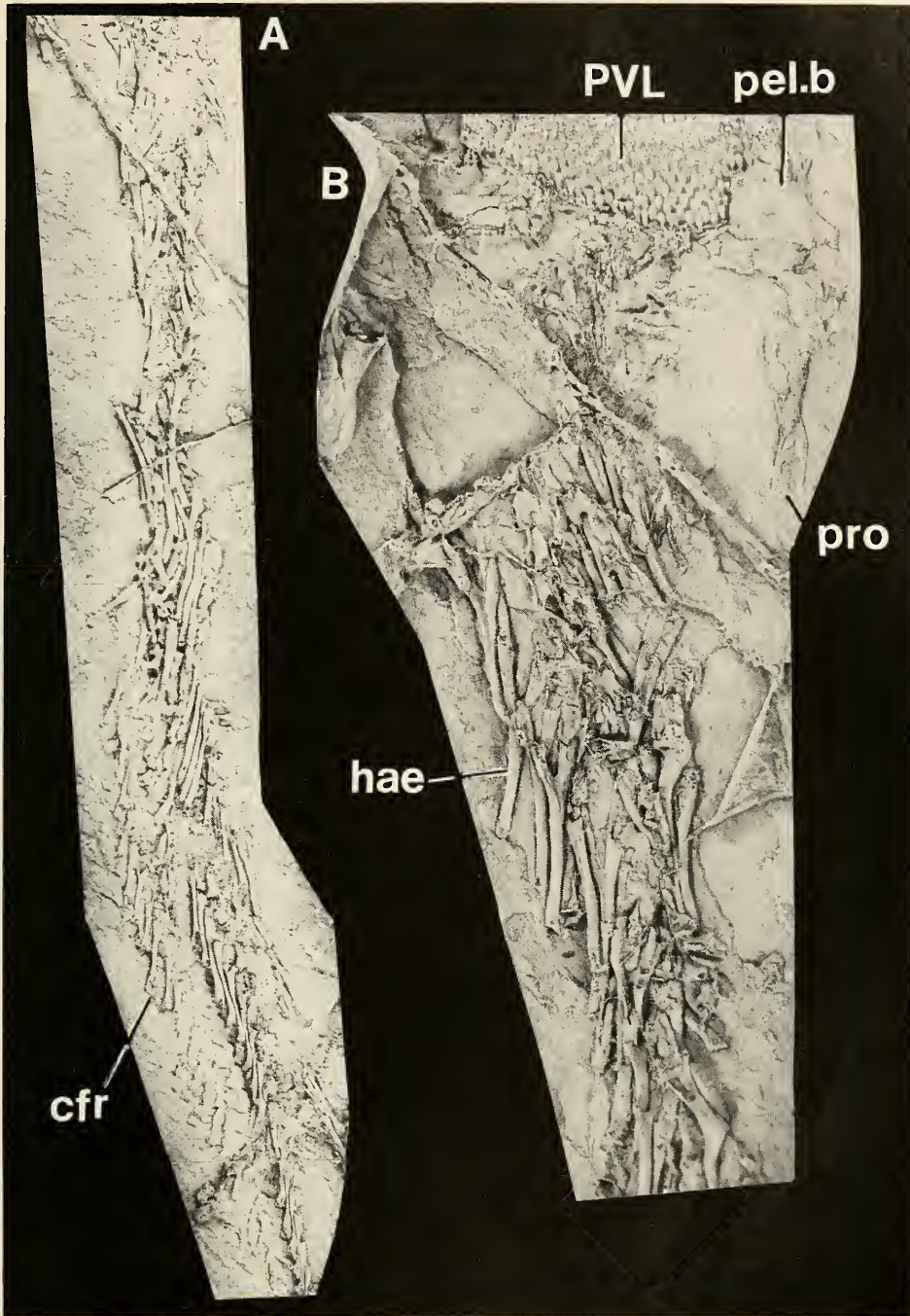
Fig. 22. Austrophyllolepis youngi gen. et sp. nov. **A,** almost entire tail, NMP 160732, × 3/4. **B,** pelvic girdle of NMP 160746, dorsal view (see also Fig. 21), × 2. Latex casts whitened with ammonium chloride. cfr, caudal fin radials; hae, haemal arch; pel.b, pelvic basal plate; pro, propterygial element of pelvic girdle; PVL, posterior ventrolateral platé.

and in the gemuendinaspid *Gemuendina* (Gross, 1963). The possession of two pairs of supragnathals is a synapomorphy uniting the euarthrodires as a monophyletic group (Miles and Young, 1977; Young, 1979; Dennis and Miles, 1983). However the euarthrodires are the largest group of placoderms and many taxa show specializations of the gnathal plates, such as the tubular ridging of *Holonema* (Miles, 1971), the durophagous gnathals of *Bullerichthys* and several other euathrodires (Dennis and Miles, 1979b), and various carnivorous adaptations of the toothplates by coccosteids and higher forms (Miles and Dennis, 1979; Dennis and Miles, 1983; Gross, 1967; Denison, 1978). The gnathals of *Groenlandaspis* are particularly interesting as there is a single median supragnathal bone, possibly formed by fusion of the anterior pair of supragnathals, giving an upper biting surface of three plates (observation of Mt Howitt *Groenlandaspis* specimens currently under study by Dr A. Ritchie). This demonstrates the potential for secondary fusion of the paired supragnathal plates in euarthrodires, and the possibility that in phyllolepids the two pairs have either fused to form one pair of supragnathals, or alternatively one pair was lost. This assumes that primitively there were two pairs of supragnathals in ancestral phyllolepids rather than one. For several reasons discussed at the end of this section I regard phyllolepids as derived from primitive euarthrodires, therefore as highly specialized placoderms. The absence of one pair of supragnathals is more acceptable as a secondary specialization than the alternative view which requires the refutation of several synapomorphies uniting phyllolepids and euarthrodires. The buccal cavities of all the known primitive euathrodires (*Kujdanowiaspis, Dicksonosteus, Groenlandaspis*) contain multicuspid tuberculate gnathal plates and similarly denticulate parasphenoids. As outgroup comparison of these features is rather weak it cannot be established if this is a plesiomorphous condition for placoderms or a synapomorphy of phyllolepids and primitive euarthrodires. The presence of lateral grooves on the parasphenoid is only known in euarthrodires and phyllolepids, although limited knowledge of the parasphenoids of other placoderms does not permit a broad enough comparison to identify this character as a synapomorphy. The distinctive non-biting division of the inferagnathal is used by Dennis and Miles (1983) and Young (1981b) to unite certain advanced brachythoracid euarthrodires. In phyllolepids this region was not ossified, and this must be regarded as representing the plesiomorphous euarthrodire condition.

Trunkshield: The most important features of the phyllolepid trunkshield are the sliding dermal neck joint and the absence of PL and PDL plates.

The dermal sliding neck joint of actinolepidoids and phyllolepids has been regarded as the primitive condition for euarthrodires, preceding the condyle and trochlear ginglymoid neck joint of the phlyctaenioid euarthrodires (Miles, 1967b; Denison, 1975). In other placoderms a dermal neck joint is present in ptyctodontids, petalichthyids, and antiarchs, with the neck joint of rhenanids being an endoskeletal articulation without dermal bone components (Young, 1980: 27). The resemblance between the dermal neck joint of ptyctodontids and petalichthyids is used by Goujet (1984) as a synapomorphy to unite these groups although Denison (1978: 39) notes that the development of this feature in petalichthyids is variable (e.g. no dermal neck joint in *Lunaspis*; vertical neck condyles in *Macropetalichthys*). Palaeacanthaspidoids and *Brindabellaspis* appear to have an endoskeletal neck articulation only, with glenoid processes present on the posterior endocranial face (Young, 1980: 27). Ørvig (1975: 49) alternatively suggests that in *Romundina* there may have been a sliding neck joint, although there is no ADL plate in the material to support this idea.

The well-developed dermal neck joints of phlyctaenioid euarthrodires is used as a synapomorphy uniting this large group of euarthrodires (Miles, 1973; Miles and Young, 1977; Young, 1979, 1981b; Dennis and Miles, 1983). Miles (1973) implies
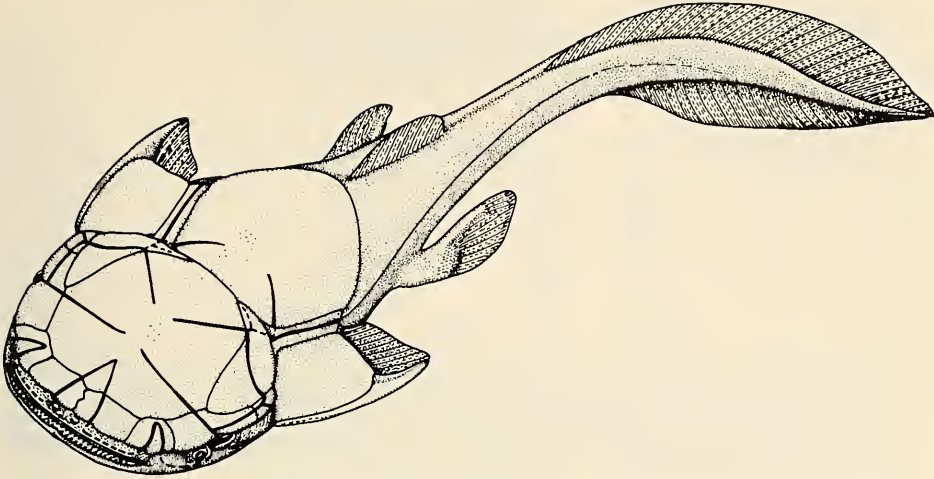
Fig. 23. *Austrophyllolepis ritchiei* gen. et sp. nov. Reconstruction of the living fish, based on a composite of all the Mt Howitt material, including details of the tail from *A. youngi*. Shape of caudal fin largely conjectural.

that the sliding neck joint of actinolepidoid euarthrodires is also a specialized character, perhaps defining a monophyletic group. The plesiomorphic condition relative to other placoderms would be the absence of a dermal neck joint. I concur with this hypothesis and, after comparison with other placoderm groups, reach the conclusion that the sliding dermal neck joint of actinolepidoids and phyllolepids is a synapomorphy of these two groups.

The absence of PL and PDL plates in the trunkshield of phyllolepids has been regarded as a plesiomorphous condition by Miles and Young (1977) and Young (1980). In antiarchs and euarthrodires the PL plate is primitively present in the trunkshield, but is later lost in some antiarchs by fusion with the PDL plate to form a mixilateral plate. In euarthrodires the PL plate primitively borders the pectoral fenestra posteriorly, and in pachyeosteomorphs the pectoral incision is open posteriorly, with the PL plate articulating with the PDL plate. A PDL plate is also found in palaeacanthaspidoids (*Kosoraspis,* Gross, 1959: *Romundina,* Ørvig, 1975) and petalichthyids (*Lunaspis,* Gross, 1961b) and is considered a primitive component of the placoderm trunkshield. The absence of the PDL plate in phyllolepids is regarded as specialized, especially when all other synapomorphies shared with euarthrodires are considered. An important distinction between the trunkshields of most other placoderms and phyllolepids is the extreme dorsoventral compression of the latter. The pectoral incision of phyllolepids does not face laterally or posterolaterally as in other placoderms, but posteriorly from the AL and AVL plates. It is a moderately large incision and cannot be regarded as primitive for euarthrodires (compare the small pectoral fenestrae of actinolepidoids such as *Bryantolepis,* Denison, 1962).

Amongst other extremely flattened euarthrodires are the homosteids and the heterosteids. In homosteids the lateral wall of the trunkshield is reduced by the loss of the PL plate, and by the unusual reduction and rearrangement of the ventral lamina (Heintz, 1968; but according to Dr E. Mark-Kurik, this plate is present on *Homostius* but somewhat reduced; pers. comm., 1983). In heterosteids the trunkshield has also undergone modifications due to compressed body form, as the pectoral incision opens posteriorly and the AL and ADL plates are fused (Ørvig, 1969: 284). It is evident that
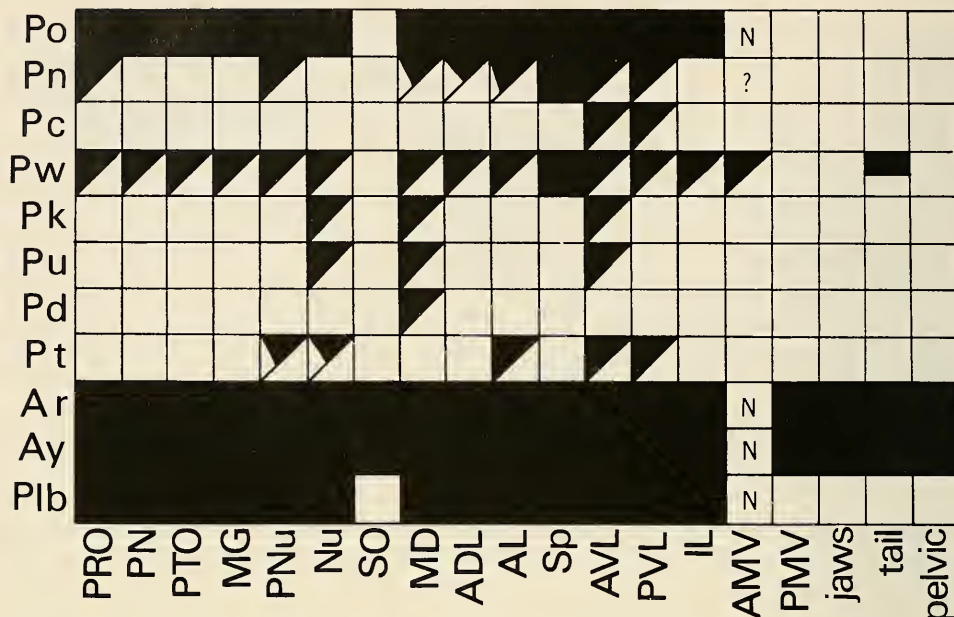
Fig. 24. Relative completeness of phyllolepid remains. Po, *Phyllolepis orvini*; Pn, *P. nielseni*; Pc, *P. concentrica*; Pw, *P. woodwardi*; Pk, *P. konincki*; Pu, *P. undulata*; Pd, *P. deliculata*; Pt, *P. tolli*; Ar, *Austrophyllolepis ritchiei*; Ay, *A. youngi*; Plb, *Placolepis budawangensis*. N indicates that this plate is probably not present in the complete armour. A fully shaded square indicates that the plate is known in both dorsal and ventral (or internal, external) views, where the top left half is shaded indicates only the dermal surface is known; the bottom left half indicates that the internal surface is known. A part of a plate surface (i.e. the complete or incomplete dorsal surface) is shown by a degree of shading of the above quadrants. Abbreviations as for Fig. 7.

the reduction and modification of the trunkshields of homosteids, heterosteids and phyllolepids relate to the constriction of space for fin and tail emergence following compression of body form. If the pectoral fin of phyllolepids extended only as far as the end of the Sp plates, as they do in *Groenlandaspis* (Dr A. Ritchie, pers. comm.) then the PL and PDL plates would have to reach the anterolaterally-facing margin of the small PVL plates. This arrangement would allow only an extremely small opening for the large tail, and thus in developing a specialized, flattened armour it is more efficient to lose certain dermal plates than constrict the unarmoured tail. It should also be noted here that the AL plates of phyllolepids cover the pectoral endogirdle and do not have a lateral component covering the body of the fish, or providing an overlap area for posterior lateral dermal trunk plates. Further specializations of the trunkshield in dorsoventrally compressed higher euarthrodires is seen in *Titanichthys* (Denison, 1978: 100). The mylostomatids are also flattened dorsoventrally although the posterior plates on the lateral wall are not well known.

The presence of either AMV or PMV plates in phyllolepids indicates that the primitive condition was probably a trunkshield with both elements present, as in euarthrodires and antiarchs. The absence of AV plates in phyllolepids was probably a parallelism with higher euarthrodires and not a shared synapomorphy in contradiction to the evidence from the dermal neck joint and other actinolepidoid synapomorphies discussed below.

The phyllolepid trunkshield resembles that of actinolepidoids in having a broad MD plate lacking a ventral keel, and a narrow ADL plate, although these features are

of little phylogenetic value. A final point concerning the trunkshield is that Goujet (1984) argues that only in phyllolepids and euarthrodires is there a separate, well-developed IL plate, and this would be another synapomorphy uniting these groups if Goujet's interpretation of the shoulder girdle in placoderms is accepted.

Tail: The tail in phyllolepids, using *Austrophyllolepis* as the only known example, was relatively long compared to the dermal armour. In other placoderm groups the tail is generally short *(Gemuendina, Lunaspis, Pterichthyodes)*. In actinolepidoids it is known completely in only one form *(Bollandaspis,* Schmidt, 1976), in which it is quite long. The tail of coccosteids is also relatively long (Miles and Westoll, 1968: fig. 48). It is concluded that a long tail relative to body size (irrespective of dermal armour size the trunk is taken from the head to the pelvic fins) is a specialized condition in placoderms. In ptyctodontids the tail region from the caudal peduncle is also extensive and this is regarded as a parallel development, particularly in view of the specialized swimming style and mode of life of ptyctodontids, which is believed to be similar to that of modern holocephalans (Miles, 1969).

The tail region in petalichthyids, rhenanids (Gross, 1961, 1963), primitive antiarchs (yunnanolepidoids, sinolepidoids; Zhang Guorui, 1978; Liu and Pan, 1958) and primitive euarthrodires *(Bollandaspis,* Schmidt, 1976; *Sigaspis,* Goujet, 1973) was covered with small scales of bony dermal denticles, this condition being primitive for placoderms. The well-preserved tail of *Austrophyllolepis* indicates that in phyllolepids the scale cover was absent. This is also seen as a specialized condition for placoderms (also seen in higher euarthrodires such as coccosteids, Miles and Westoll, 1968, and in higher antiarchs such as bothriolepids, Stensiö, 1948; Long, 1983a).

The unique pelvic girdle of phyllolepids is interpreted as an autapomorphy for the group. In primitive euarthrodires *(Sigaspis, Kujdanowiaspis,* Dr Goujet, pers. comm.) the pelvic endogirdle was closely associated with the scales immediately behind the trunkshield, whereas in higher euarthrodires the pelvic endogirdle is a completely internal perichondral ossification with long iliac processes (Miles and Westoll, 1968; Dennis and Miles, 1982). The close association of the phyllolepid basal pelvic plate with the trunkshield is similar to the primitive euarthrodire condition, and differs in this respect from the pelvic girdles of all other placoderm groups (Stensiö, 1969: figs 245-247).

RELATIONSHIPS OF PHYLLOLEPIDS

From the above discussion of phyllolepid character states I proposed that phyllolepids and euarthrodires are a monophyletic group which share the following synapomorphies: 1, endocranium with well-produced posterior postorbital processes; 2, endocranium with proportionately large cucullaris fossa; 3, endocranium primitively with separate ethmoid and postethmoid divisions which is reflected in the dermal snout bones as a separate rostral capsule; 4, headshield with a single large pair of PNu plates which contain the junction of the occipital and posterior pit lines and the main lateral line canal; 5, headshield with an extensive dermal thickening above the optic capsule. In addition Goujet (1984) unites phyllolepids and euarthrodires by 6, the possession of a true IL plate (assuming Goujet's interpretation of the IL plates of palaeacanthaspidoids and yunnanolepidoids is correct). Furthermore there are histological similarities between phyllolepid dermal bones and those of euarthrodires, recognized earlier by Stensiö (1934) and Gross (1934). Other characters shared by phyllolepids and euarthrodires, such as a large parasphenoid with lateral grooves, may prove useful in phylogenetic analysis when more is known about the anatomy of other placoderms. Phyllolepids and actinolepidoid euarthrodires (including *Wuttagoonaspis*)
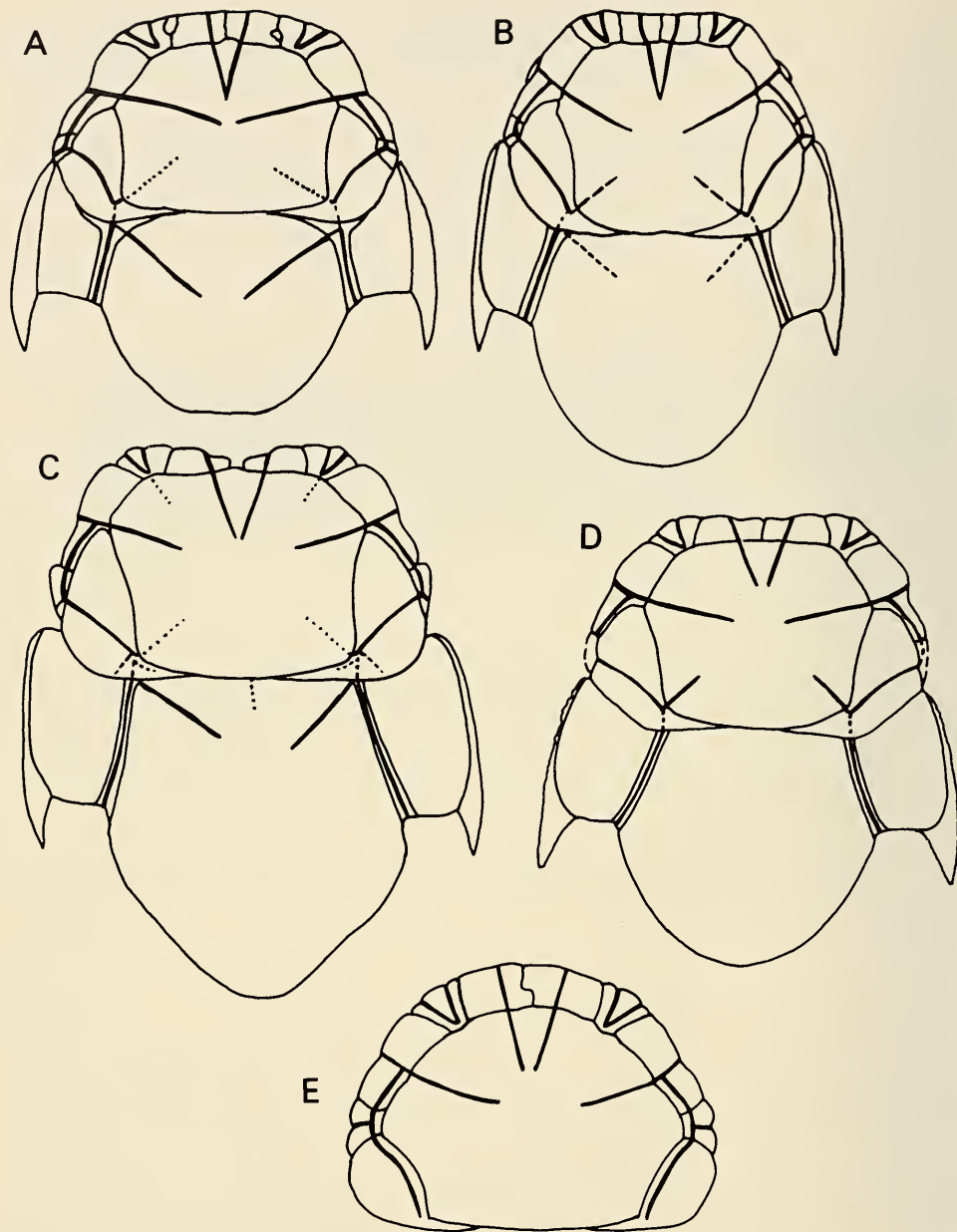
Fig. 25. Comparison of phyllolepid dorsal armours. **A**, *Austrophyllolepis ritchiei*, gen. et sp. nov. **B**, *A. youngi*, gen. et sp. nov. **C**, *Phyllolepis orvini* (after Stensiö, 1936). **D**, *P. woodwardi* (after Stensiö, 1939). **E**. *Placolepis budawangensis* (after Ritchie, 1984).

are united by 7, the possession of a sliding dermal neck joint; and 8, having PTO plates often larger, but never smaller, than the MG plates of the headshield.

The Euarthrodira as currently defined by Young (1979: 342) share (a) two pairs of supragnathals, (b) distinct posterolateral corners on the headshield (also shared with antiarchs, Young and Gorter, 1981; Dennis and Miles, 1983) (c) separate endocranial postorbital processes, (d) cucullaris fossa well developed, (e) paravagal fossa reduced or absent and (f) trunkshield incorporating a PL plate that encloses a pectoral fenestra. As stated in the previous section, the primitive phyllolepid trunkshield is assumed to have possessed PL plates. Phyllolepids appear to share the endocranial features of euarthrodires as far as reconstruction allows (although the presence of a paravagal fossa is indeterminate). The presence of one pair of supragnathals in phyllolepids is a character which may separate phyllolepids from euarthrodires if this is the primitive phyllolepid condition. Phyllolepids could in this case remain as a sister group to euarthrodires rather than a subgroup of the Actinolepidoidei, although this hypothesis would imply that a sliding dermal neck joint was independently acquired along with reduction of the MG plate in actinolepidoids. Alternatively it is feasible that one of the pairs of upper jaw toothplates was lost or fused in phyllolepids, as in *Groenlandaspis*. The diversity and complexity of the euarthrodiran gnathal apparatus (Miles, 1969; Ørvig, 1980; White, 1978), and the variations seen in the jaws of other fish groups (e.g. Holocephali, Actinopterygii) leave this question open, especially in view of our incomplete knowledge of the jaws of primitive euarthrodires. I leave the possession of two pairs of supragnathals as a synapomorphy of the euarthrodira (and possibly primitive phyllolepids), but maintain that, on the grounds of shared synapomorphies 1-8, phyllolepids are more probably a subgroup rather than a sister group of euarthrodires.

The hypotheses of Miles and Young (1977) and Young (1980), which place phyllolepids as the sister group to antiarchs and euarthrodires, use two characters to unite these groups: the presence of PL plates and PMV plates (assuming Gross's interpretation of *Lunaspis,* Gross 1961, is incorrect). Young and Gorter (1981) and Dennis and Miles (1983) add the presence of a well-developed obstantic margin (correlated with the broad posterolateral breadth of the headshield) as a synapomorphy of antiarchs and euarthrodires. In the previous discussion I have considered the problem of the PL plate, and I believe that the presence of a PMV plate in *Austrophyllolepis* clearly dismisses this feature as being restricted to antiarchs and euarthrodires. The broad posterolateral corners on the headshields of antiarchs and euarthrodires is only seen in the primitive members, or those retaining plesiomorphic characters, such as yunnanolepidoids, sinolepidoids, bothriolepidoids, actinolepidoids, phlyctaeniids and most brachythoracids. In specialized groups there is a secondary loss of this feature as headshield shape changes, for example, in asterolepidoids and some higher brachythoracids such as *Leptosteus, Oxyosteus, Belosteus, Brachydeirus* and *Synauchenia* (Denison, 1978). From this it can be deduced that if phyllolepids are specialized actinolepidoids it is possible that changes in the basic headshield shape, such as dorsoventral flattening, resulted in parallel secondary loss of the distinctive posterolateral corners. Once a sister group relationship for phyllolepids and euarthrodires is accepted there are several possible hypotheses of relationship for phyllolepids, actinolepids, *Wuttagoonaspis* and *Antarctaspis* (Fig. 26).

The actinolepidoids are regarded as the plesion sister group to other euarthrodires by Young (1981b) and Dennis and Miles (1983). Miles (1973) believed that actinolepidoids were a monophyletic group sharing a sliding neck joint. In addition to synapomorphies shared by actinolepidoids, phyllolepids and *Wuttagoonaspis* discussed above, the actinolepids share two additional synapomorphies: 9, a supraorbital process on the endocranium, and 10, AV plates.
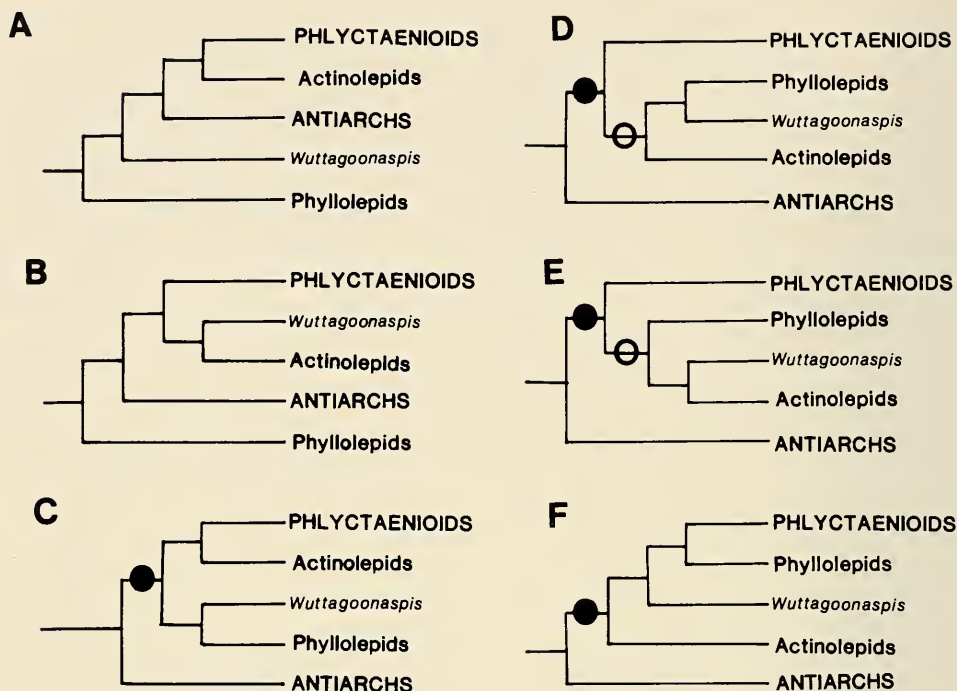
Fig. 26. Alternative hypotheses of relationships for phlyctaenioids, actinolepids, phyllolepids, *Wuttagoonaspis* and antiarchs. All synapomorphies listed in the caption to Fig. 27. **A,** hypothesis of Young (1980), excludes *Wuttagoonaspis* and phyllolepids from the euarthrodires and antiarchs because of the absence of broad posterolateral corners on the headshield (and obstantic margin, Young and Gorter, 1981), and absence of posterior lateral plates (not really known for *Wuttagoonaspis*). **B,** hypothesis of Miles and Young (1977) includes *Wuttagoonaspis* within the euarthrodires as a separate group of actinolepidoids. Hypotheses **C-F** assume monophyly of phyllolepids, *Wuttagoonaspis* and euarthrodires (shared synapomorphies 1-5; black circle). Hypothesis **C** involves either an independent acquisition of a sliding neck joint in actinolepids or its loss in phlyctaenioids, and a parallel acquisition of anterior ventral plates in *Wuttagoonaspis* and actinolepids. Hypotheses **D** and **E** assume monophyly of actinolepids, phyllolepids and *Wuttagoonaspis* using synapomorphies 6 and 7 (open circles). Hypothesis **D** proposes a sister group relationship between phyllolepids and *Wuttagoonaspis* using synapomorphies 12 and 13 (possibly 14). This also involves independent loss of anterior ventral plates in phyllolepids and phlyctaenioids. Hypothesis **E** unites *Wuttagoonaspis* and actinolepids by synapomorphy 9, but imples that the highly reduced marginal plates, small orbits (and possibly undifferentiated centronuchal plate) were acquired and lost in actinolepids. Hypothesis **F** assumes that the loss of anterior ventral plates in phyllolepids and phlyctaenioids was a synapomorphy, but involves the independent loss of synapomorphies 12, 13 (possibly 14) in phlyctaenioids.

Wuttagoonaspis is regarded as an actinolepidoid because it has a sliding dermal neck joint and AV plates (Dr A. Ritchie, pers. comm.). *Wuttagoonaspis* can be united with phyllolepids and *Antarctaspis* if the undifferentiated centronuchal area on the headshield is a valid synapomorphy. However, as this condition is also seen in an undescribed actinolepid from Severnaya Zemlya (Dr D. Goujet, pers. comm.) I regard this feature as too unstable a character for the study of relationships. *Antarctaspis, Wuttagoonaspis* and phyllolepids show similar specializations in the reduction of the orbits and small size of the MG plates. *Wuttagoonaspis* differs from phyllolepids and actinolepidoids in the unusual dermal skull roof pattern, although it still shares the basic pattern of paired PRO, PN, PTO, PMG and PNu plates (possibly with separate MG plates). The

endocranium of *Wuttagoonaspis* is not divided into separate postethmoid and rhinocapsular ossifications (Ritchie, 1973) representing an apomorphic condition relative to phyllolepids and other actinolepidoids. On the existing evidence I relate *Wuttagoonaspis* to phyllolepids tentatively by the large Nu plate, reduced MG plate, and small orbits (possibly also by the meandrine ridge ornamentation), but regard *Wuttagoonaspis* as belonging to an aberrant group of specialized actinolepidoids which diverged from the main stock at an early stage. The absence of broad posterolateral corners on the headshield of *Wuttagoonaspis* (Young and Gorter, 1981) may be due to secondary changes in headshield shape such as occipital elongation.

Antarctaspis is too poorly known to be placed confidently in the cladogram. In the absence of other information I corroborate Denison's opinion (1978) that *Antarctaspis* is more closely related to phyllolepids than to other placoderms by sharing a large Ce-Nu plate and reduced MG plates.

Within the actinolepids there is much variation in the length and contact relationships of the Nu plate, size and degree of ossification of the dermal nasal capsule bones, and trunkshield shape. Actinolepids with a long Nu plate are regarded as plesiomorphic within the group by comparison with other placoderm groups. Petalichthyids possess a long Nu plate in contact with the PRO plates; primitive antiarchs possess a long Nu plate (yunnanolepidoids and sinolepidoids) and some palaeacanthaspidoids and related forms possess long Nu plates, such as *Brindabellaspis, Kimaspis, Romundina,* and *Kosoraspis* (Young, 1980; Mark-Kurik, 1973; Ørvig, 1975; Gross, 1959). The actinolepids possessing a long Nu plate in contact with the PRO plates (*Aethaspis, Proaethaspis* and *Baringaspis,* Denison, 1958; Miles, 1973) are considered as the plesion sister group to other actinolepids. Actinolepids with a long Nu plate not in contact with the PRO plates (*Stuertzaspis* and *Heightingtonaspis,* Westoll and Miles, 1963; White, 1969) are presumably less specialized than those with short Nu plates, and often other specializations such as broadened or lengthened armour (*Bryantolepis* and other actinolepids; Denison, 1978; Liu, 1979).

The resulting cladogram recognizes phyllolepids and *Wuttagoonaspis* as specialized lineages of the actinolepidoids. This hypothesis will no doubt be testable as new Devonian faunas are described from Australia and Antarctica where ancestral phyllolepids might be expected (Young, 1981a: 237). A final auxiliary criterion for assessing phylogenetic relationships, but one that has been strongly criticized or misused, is that of geological character precedence (Wiley, 1981: 148). Phyllolepids occur late in the geological record (Frasnian-Famennian) whereas the earliest antiarchs and euarthrodires appear in the Early Devonian (Siegenian, earlier for antiarchs, Pan Kiang, 1981), some thirty million years before. The unique specializations of phyllolepids within the Placodermi, such as otoliths and the absence of dermal nasal capsule bones, and their widespread distribution indicate that they are not primitive within the Placodermi, but are one of the most specialized and successful groups. The late appearance of phyllolepids suggests their derivation from actinolepids probably during the late Middle Devonian, and their successful dispersal from an east Gondwana source (Young, 1981a) probably during the Frasnian. The most specialized phyllolepids *(Phyllolepis orvini)* occur in the Famennian of East Greenland. This is comparable with the bothriolepid distribution pattern in which the most primitive species occur early in Australia and the most specialized forms (including *Bothriolepis groenlandica*) occur late in Europe and Greenland (Long, 1983a).

With the Phyllolepidae the relationships of *Placolepis, Austrophyllolepis* and *Phyllolepis* are determined by using actinolepidoids for outgroup comparison. Only *Phyllolepis orvini, P. woodwardi,* both species of *Austrophyllolepis,* and *Placolepis budawangensis* are relatively well known (Fig. 24), and so comments about the in-

terrelationships of phyllolepids will be confined to these taxa. Fig. 25 illustrates the major differences in the dorsal aspects of the dermal armour of these phyllolepids.

It has been shown that a small MG plate is a specialized condition within the actinolepidoids, and therefore the large MG plate of *Placolepis* is regarded as plesiomorphic relative to *Austrophyllolepis* and *Phyllolepis*. The entry of the main lateral line canal into the PNu plate is anteriorly located in all actinolepidoids and *Placolepis,* whereas *Austrophyllolepis* and *Phyllolepis* are specialized in having the lateral line canal entering the PNu from about midway along the plate, and the MG plate separated from the centronuchal area by the PNu plate. In these respects I regard *Placolepis* as the plesiomorphic sister group to *Austrophyllolepis* and *Phyllolepis*. The most specialized of the phyllolepids is *Phyllolepis orvini* which has a pair of small PRO plates separated from each other medially in the mature armour. The large size of this species is another apomorphic feature relative to other phyllolepids. The trunkshields of *Placolepis* and *Phyllolepis orvini* are here considered as specialized in their absence of median ventral plates. *Austrophyllolepis* retains a PMV plate as a plesiomorphic character. It is more parsimonious to unite *Austrophyllolepis* and *Phyllolepis* by at least two shared synapomorphies of the headshield than to unite one species of *Phyllolepis* and *Placolepis* by the loss of the PMV plate. I envisage the ancestral phyllolepid as possessing two median ventral plates in the trunkshield with a headshield similar to that of *Placolepis,* but probably having smaller PN plates, or even differentiated Ce and Nu plates.

FUNCTIONAL MORPHOLOGY AND LIFESTYLE OF PHYLLOLEPIDS

The flattened body form of phyllolepids reflects a sedentary demersal lifestyle, paralleled by many other groups of fishes such as psammosteid heterostracans, gemuendinoid rhenanids, batoid chondrichthyans and pleuronectiform teleosteans.

Fig. 27. The most economical hypothesis of phyllolepid relationships. This involves accepting two assumptions (that primitive phyllolepids possessed posterior lateral plates and two pairs of superagnathals) on the evidence that phyllolepids and euarthrodires are more closely related than are antiarchs and euarthrodires because of synapomorphies 1-6. Synapomorphy scheme: A. Primitively possessing posterior lateral plates, headshield with broad posterolateral corners, posterior median ventral plate present. B. 1. Endocranium with well produced posterior postorbital processes. 2. Endocranium with large cucullaris fossa (1/3-1/2 total endocranial length). 3. Endocranium with separate rhinocapsular and postethmoid divisions, reflected in the arrangement of the anterior dermal headshield bones. 4. Single large pair of paranuchal plates with junction of the posterior pit-line, occipital pit-line and main lateral line canal; receiving the main lateral line canal from the marginal plate. 5. Extensive dermal bone thickening above optic capsules on headshield. 6. True interolateral plates present (*sensu* Goujet, 1984). C. 7. Sliding dermal neck joint. 8. Postorbital plates generally larger than marginal plates, (possible synapomorphies: a, long tail; b, denticulated tooth plates). D. Ginglymoid neck joint and other synapomorphies listed in Young (1981b) and Dennis-Bryan and Miles (1983). E. 9. Supraorbital process on endocranium (Dr D. Goujet, pers. comm.). 10. Anterior ventral plates present. F. 11. Nuchal plate not contacting preorbitals (separate nuchal and central plates assumed). G. 12. Nuchal plate shortened considerably (and various autapomorphies, e.g. broadened armour in *Bryantolepis*). H. 13. Greatly reduced marginal plates. 14. Diminution of orbital size, and possibly synapomorphy 15. I. 15. Combined centronuchal plate (or undifferentiated centronuchal area). 16. Postorbital plate narrow with long anterior and posterior divisions divided by the central sensory line canal. J. 17. Incorporation of postnasal plate into position between preorbital and postorbital plates. 18. Endocranium probably cartilaginous. 19. Absence of rostral and pineal plates. 20. Reduction or loss of postmarginal plate. 21. Body form dorsoventrally flattened (might corroborate synapomorphy 22). 22. Loss of posterior dorsolateral and posterior lateral plates. 23. Secretion of saccular otoliths. 24. Specialized pelvic girdle with long propterygia. K. 25. Further reduction of marginal plate size. 26. Marginal plate separated from nuchal plate by enlarged paranuchal plates. 27. Paranuchal plates with entry of main lateral line canal more posteriorly situated (70-50% of plate length). 28. External posterior margin of postnasal plate larger. L. 29. Elongated smaller marginal plate. 30. Postnasal plate with even larger posterior external margin. M. Autapomorphies of *Phyllolepis orvini* 31. Large size attained. 32. Separation of preorbital plates from mesial contact. X:loss of anterior median ventral plate; Y: loss of posterior median ventral plate.
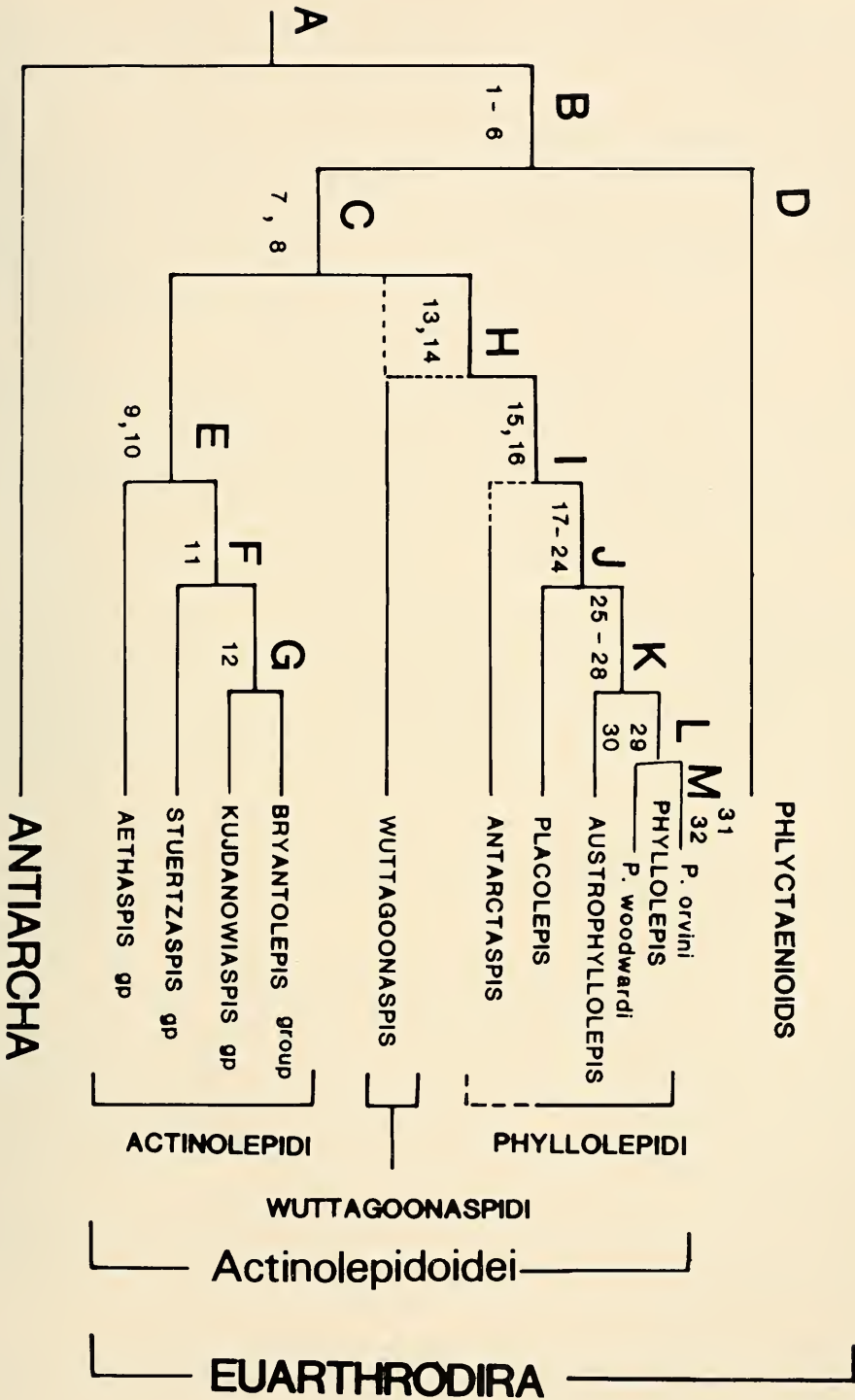
Fishes with depressiform bodies generally have small tails as there is no need for strong forward propulsion unless the head is streamlined for stability during swimming. A flat body is unsuitable for fast motion unless excessive lift is countered by large, manoeuvrable pectoral fins (Harris, 1938; Alexander, 1967). A long tail without macromeric squamation, as in phyllolepids, would result in a subanguilliform swimming style with a strong yawing effect. The unusual combination of a depressed body shape with a long tail is probably an adaptation for a fast take-off from a static benthic position. Unlike batoids and pleuronectiforms the take-off could not be initiated by pectoral fin undulation (Aleev, 1969), but relied on the powerful pushing action of the long tail. Further adaptation for a powerful thrust is seen in the axial skeleton of phyllolepids which is strengthened by articulating zygapophyses of the neural arches, as in coccosteid and higher euarthrodires (Stensiö, 1969: fig. 176).

The jaws and parasphenoid of phyllolepids indicate that the buccal cavity was large and adapted for gripping food rather than crushing, cutting, slicing or triturating. A gripping dentition implies the ability to catch active prey. The phyllolepid mouth was subterminal from the position of the toothplates, and the gape was probably restricted by the inefficient dermal neck joint and endocranial autostyly. A consideration of available food sources from the Mt Howitt deposit indicates that *Austrophyllolepis* probably fed on either soft mobile invertebrates or other fishes, most likely juvenile placoderms which swam close to the bottom of the lake.

The extensive dorsal laterosensory field of phyllolepids is associated with the formation of otoliths within the saccular cavities, and the absence of an open endolymphatic duct on the PNu plates. Otoliths act as statolith bodies responsive to any movements of water. In stationary fish this is advantageous for the detection of prey or predators especially in murky environments where vision is impeded (Lowenstein, 1971; Alexander, 1967). These features suggest strongly that phyllolepids were specialized benthic predators which relied more on an advanced acoustico-lateralis system than either vision or olfaction to detect prey. The reduced orbits of phyllolepids, and presumably reduced olfactory capsules, would be of little use in murky benthic habitats. I suggest that phyllolepids may have been slightly buried in the substrate waiting for unsuspecting prey to come swimming above them. The long tail of phyllolepids would provide the sudden thrust necessary to lurch up and catch the prey with the gripping dentition.

CLASSIFICATION AND FORMAL SYSTEMATICS
Order EUARTHRODIRA Gross 1932

Diagnosis: Placoderm fishes which primitively possess headshields with distinctive posterolateral corners and long obstantic margins; two pairs of supragnathals; endocranium perichondrally ossified or cartilaginous with well produced separate posterior postorbital processes, and a proportionately large cucullaris fossa; paravagal fossa reduced or absent. Trunkshield primitively with PL plates enclosing a small pectoral fenestra.

Remarks: The diagnosis of Young (1979: 344) is amended to include phyllolepid features described in this paper whilst accepting two assumptions of phyllolepid plesiomorphy: that PL plates and two pairs of supragnathals were probably present in primitive phyllolepids.

Suborder ACTINOLEPIDOIDEI Miles and Young 1977

Diagnosis: Euarthrodire placoderms which possess a sliding dermal neck joint and generally have a MG plate smaller than the PTO plate.

Infraorder: ACTINOLEPIDI Miles and Young 1977

Diagnosis: Actinolepidoid euarthrodires possessing AV plates and a supraorbital process on the endocranium.

Infraorder: WUTTAGOONASPIDI Miles and Young 1977

Diagnosis: Actinolepidoid euarthrodires possessing a long headshield with reduced orbits, small MG plates which may be incorporated or fused with the PTO plates and a long paraorbital plate below the orbit. AV plates present.

Remarks: This diagnosis is a short summary of the intrinsic characters of *Wuttagoonaspis* used in the above hypothesis of relationships. It will undoubtedly require amendment when this interesting genus is described in more detail.

Infraorder: PHYLLOLEPIDI nov.

Diagnosis: Actinolepidoid euarthrodires possessing a broad armour with an undifferentiated centronuchal area, and large PN plates between the PRO and PTO plates in contact with the Nu plate. Endocranium cartilaginous with ossified broad parasphenoid. Single pair of supragnathals present. Dermal cheek bones reduced to a single small SO element. Trunkshield of specialized forms without PL and PDL plates. Tail long, without scale cover, and long caudal fin. Pelvic girdle with long propterygial element.

Remarks: Diagnoses of the genus *Austrophyllolepis* and two species *A. ritchiei* and *A. youngi* are given and discussed in the section entitled systematic descriptions. Stensiö (1939) diagnosed the various species of the genus *Phyllolepis* and Ritchie (1984) has diagnosed *Placolepis budawangensis*. The order Phyllolepida Stensiö (1934) is made redundant, although the family Phyllolepidae Woodward (1891) can remain as a subdivision of the infraorder Phyllolepidi to include *Phyllolepis* and *Austrophyllolepis* until new material of phyllolepids comes to hand warranting revision of this scheme.

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